

UNITED STATES DEPARTMENT OF THE INTERIOR  
GEOLOGICAL SURVEY

SHORT PAPERS  
FOR THE  
SECOND INTERNATIONAL SYMPOSIUM ON THE CAMBRIAN SYSTEM  
1981

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Editor

Open-File Report 81-743

Technical sessions held August 9-13, 1981, at the  
Colorado School of Mines, Golden, Colorado,  
United States of America

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## SECOND INTERNATIONAL SYMPOSIUM ON THE CAMBRIAN SYSTEM

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### PROGRAM

Field Trip 1. Cambrian Stratigraphy and Paleontology of the Great Basin and vicinity, western United States. July 30 to August 9, 1981.

Technical Sessions. Colorado School of Mines, Golden, Colorado. August 9-13, 1981.

Field Trip 2. The Cambrian System in the Canadian Rocky Mountains, Alberta and British Columbia. August 14-20, 1981.

Field Trip 3. Cambrian and Lowest Ordovician Lithostratigraphy and Biostratigraphy of Southern Oklahoma and Central Texas. August 14-19, 1981.



## PREFACE

The Cambrian System holds special scientific interest because it contains the primary record of the earliest evolutionary diversification of metazoan life on Earth. Study of the patterns of evolutionary diversification and associated environmental conditions provides our understanding of the original colonization of the Earth's marine ecosystem by complex plant and animal communities.

Rocks of Cambrian age contain a significant portion of the world's sedimentary and metallic mineral resources. Increased understanding of Cambrian stratigraphy, depositional environments, and paleogeography improves our ability to discover new deposits which are so necessary to the agricultural and industrial well being of the world's human population.

This volume is the proceedings of the technical sessions of the Second International Symposium on the Cambrian System, held August 9-13, 1981, in Golden, Colorado. The first international Cambrian symposium was held in conjunction with the 20th International Geological Congress in Mexico City in 1956. Since 1956, a wealth of research on Cambrian stratigraphy and paleontology has been conducted in all parts of the world. This volume contains a sample of that work in 72 scientific reports authored or coauthored by 95 research scientists. Thirteen countries are represented by the contributors, including the United States of America (37), the Union of Soviet Socialist Republics (16), the People's Republic of China (12), England (6), Australia (5), Sweden (5), Canada (3), France (3), Argentina (2), Estonia (2), West Germany (2), South Korea (1), and Poland (1).

This volume was edited and published with a lead time of less than three months from the time manuscripts were received from authors. Reports were technically reviewed by at least two specialists, and edited and proofread by the editor, who assumes all responsibility for errors in the published version of the authors' original texts.

Production of this proceedings volume in such a short period of time would not have been possible without the dedicated effort of Julia E. H. Taylor, Leonard A. Wilson, and a group of very capable publications specialists and typists from the U.S. Geological Survey in Denver, Colorado.

Michael E. Taylor, Editor

June 12, 1981

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# 1. THE PRECAMBRIAN-LOWER CAMBRIAN FORMATIONS OF NORTHWESTERN ARGENTINA

By

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For many years, a large area of slightly metamorphosed outcrop in northern Argentina (fig. 1) was considered to be of Precambrian age. The outcrop area extends from near the Argentinian-Bolivian border to 25° south latitude. The most significant fact indicating the age of these rocks is that they lie in angular unconformity beneath a fossiliferous sedimentary sequence of Cambrian-Ordovician age (fig. 2). To the south the outcrops are connected with highly metamorphosed rocks, which presumably represent part of the South American Precambrian craton. The studies of Keidel (1947) represent a line of thought, well established in Argentine geology, which attributed these outcrops to the Precambrian.

However, during the last decade, radiometric investigations of crystalline rocks and the discovery of ichnofossils of Cambrian age (table 1) have required the revision of age interpretations and the elaboration of new ideas regarding the geosynclinal evolution of the western margin of the South American continent.

## STRATIGRAPHY

The principal stratigraphic units exposed in northwestern Argentina are described as follows:

**1, Puncoviscana Formation:** This formation is exposed from the north end of the Sierra de Santa Victoria at the border with Bolivia to the south end of Salta Province; its western outcrops are in the Sierra de Cobres (66° 30' W.), and the eastern extent is in Sierra de La Candelaria (64° 30' W.). Turner (1960) described the formation as a unit formed by slates, phyllites, limestones, conglomerates, and quartzites, ranging from dark gray to grayish red. The type locality is in Sierra de Santa Victoria. The formation is affected by intense folding. This fact makes difficult any determination of the total thickness of the sequence. Miller (1979) studied the deformation of this unit and determined, by means of microstructural measurements, that the general trend of the orogene was NNE-SSW to NE-SW.

According to Salfity and others (1975) it is possible to include this unit in the Lerma Group, which can be characterized lithostratigraphically in the Valle de Lerma (Salta Province). It is formed by the

following formations (in ascending order): Sancha (shales and slates), Volcan-Las Tienditas (dark limestones), Puncoviscana (shales and slates), and Corralito (conglomerates).

Shales of the Puncoviscana Formation have provided abundant trace fossils in several localities in Salta and Jujuy Provinces (table 1). They helped to confirm that this unit is in part Lower Cambrian (Aceñolaza, 1978).

Typically, this formation is composed of graywackes and pelitic rocks with rhythmic structures. These rocks were affected by low-grade metamorphic processes in the Cordillera Oriental (Toselli, 1980).

**2, Suncho Formation:** The Suncho Formation is exposed in the Sierra de la Ovejera (Catamarca Province), about 250 km southwest of Tucuman, in a tectonic block bounded by Ordovician granites which

Table 1.--Distribution of Lower Cambrian Ichnogenera in northern Argentina.

	Localities						
	1	2	3	4	5	6	7
<b>Cochlichnus</b>				*		*	
<b>Dimorphichnus</b>						*	
<b>Diplichnites</b>					*	*	
<b>Glockeria</b>				*			
<b>Gordia</b>	*	*	*			*	*
<b>Helminthopsis</b>			*	*		*	
<b>Nereites</b>				*	*		*
<b>Oldhamia</b>	*	*				*	
<b>Planolites</b>	*	*	*	*	*	*	*
<b>Protichnites</b>						*	
<b>Protovirgularia</b>			*				
<b>Tasmanadia</b>				*			
<b>Torrowangea</b>				*			

Localities: 1, Sierra Ovejera (Catamarca); 2, San Antonio de los Cobres (Salta); 3, Cachi (Salta); 4, Salta; 5, Purmamarca (Jujuy); 6, Munano (Salta); 7, Campo Quijano (Salta).

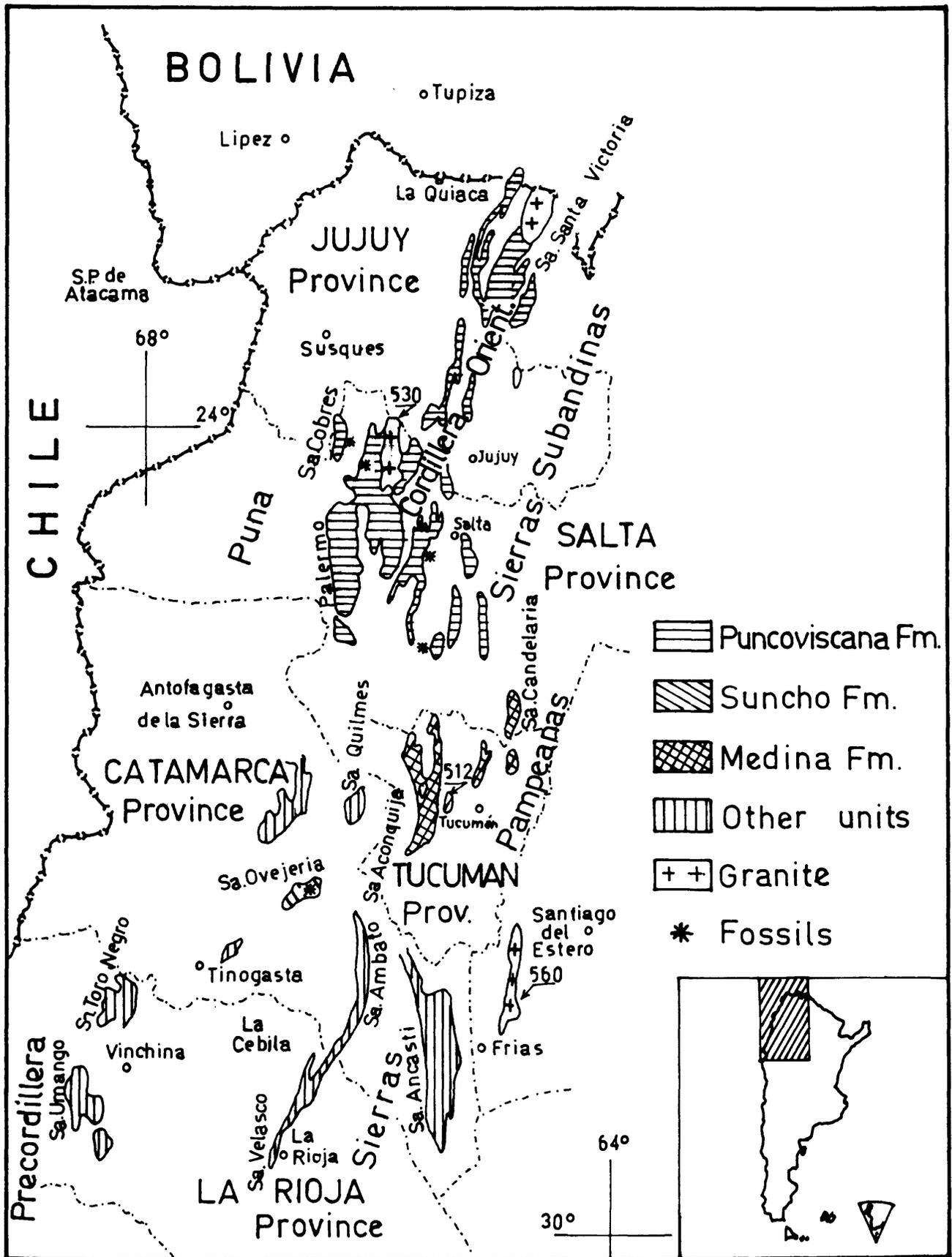


Figure 1.--Outcrops of upper Precambrian-Cambrian formations and Ordovician granite in northern Argentina. Sa., Sierra.

have been intruded by Cenozoic volcanites. The formation was first described by Mirre and Acenolaza (1972) and was later studied in detail by Durand (1980). The formation contains slates and graywackes with rhythmic structures and several levels with trace fossils (table 1). The metamorphic grade of this formation is almost equivalent to that of the Puncoviscana.

**3, Medina and San Javier Formations:** These formations have been described by Bossi (1969) and Toselli and others (1972) from outcrops in the Tucuman Province. The structural and lithostratigraphic characters shown are the same as those of the Suncho; no fossils have been found in either the Medina or the San Javier. The whole-rock radiometric determinations performed on the San Javier (512 m.y.) and the Medina (570 m.y.) indicate only the age of metamorphism.

**4, Other Units:** On the basis of mineralogic characteristics and structural complexities, the gneisses and schists from Aconquija and Cumbres Calchaquies (Rossi de Toselli and Toselli, 1979) can be considered as equivalents of the formations described above (age of sedimentation, not metamorphism) as can the quartz-micaceous schist from the Ancasti Formation (Acenolaza and others, 1980) and the La Cebila Formation (Espizua and Caminos, 1979) in Catamarca and La Rioja Provinces. The sedimentation of metamorphosed rocks in Maz-Umango, Toro Negro, in La Rioja, also belongs to this cycle (Caminos, 1979).

#### STRATIGRAPHIC CONSIDERATIONS

In the author's opinion the sedimentary cycle during which these rocks were deposited began in late Precambrian times (approximately 900 m.y. B.P.) and lasted until the Middle to Late Cambrian age (530 m.y. B.P.). The sedimentary basin bordered the La Plata River craton to the west; toward the north it was situated between the Arequipa craton and the Brazilian craton. Unfortunately, it is not yet possible to clearly define evolution and development of the basin because of tectonic complexities. It must be pointed out that the main orogenic event occurred during the Late Cambrian, as can be determined from several sedimentary sequences in southern South America (Acenolaza and Miller, 1980)

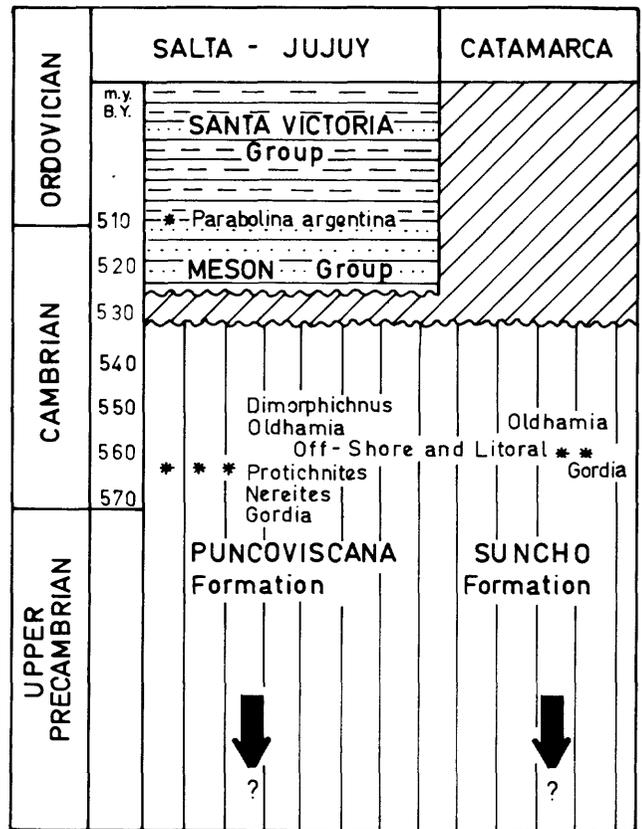


Figure 2.--Correlation of selected upper Precambrian through Lower Ordovician units in Salta, Jujuy, and Catamarca Provinces, northern Argentina.

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## 2. PTYCHOPARIID TRILOBITES IN THE LOWER CAMBRIAN OF SCANDINAVIA

By

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In Scandinavia, the Lower Cambrian biostratigraphic framework is based mainly upon the succession of trilobites. A review of the Lower Cambrian biostratigraphy, as employed in Scandinavia, has been presented by Bergström (1980). The zonal scheme proposed in this study is based mainly on the sequence in the Mjøsa area, southern Norway, and in Skåne (Scania), southern Sweden. At present the Early Cambrian faunal succession in Scandinavia is divided into five zones. The conventionally lowermost zone is characterized by the occurrence of non-trilobite fossils such as Platysolenites antiquissimus and hyolithids (Bergström, 1980 and this volume). In the Dividal Group of northern Scandinavia, these fossils may be associated with Spirosolenites and Aldanella (Fjyn and Glaessner, 1979). The four successive Lower Cambrian zones have been named after characteristic trilobites, in ascending order: Schmidtellus mickwitzii and Holmia mobergi, Holmia n. sp., Holmia kjerulfi (including a group of closely related forms), and Proampyx linnarssoni. The significance of the two uppermost zones, in terms of international correlation, is discussed by Bergström and Ahlberg (1981).

In contrast to the underlying zones, the Holmia kjerulfi Zone contains well differentiated faunas. The faunal elements include, amongst others: Holmia kjerulfi and closely related species, Calodiscus lobatus?, various inarticulate brachiopods, hyolithid and helcionellid mollusks, and species of Indiana? and Hylolithellus. However, in many localities the bulk of the fauna is made up of ptychopariid trilobites. In Scandinavia the Holmia kjerulfi Zone marks the earliest appearance yet recorded for a number of ptychopariid trilobites. Ptychopariid trilobites are also a substantial component of the fairly rich and diverse faunas of the Proampyx linnarssoni Zone.

The ptychopariid trilobites from the Lower Cambrian of Scandinavia tend to be smooth, generalized trilobites. They have been treated in a monograph by Ahlberg and Bergström (1978), who referred all forms to the subfamily Ellipsocephalinae of the family Solenopleuridae.

### OCCURRENCE OF GENERA

The available Lower Cambrian ptychopariid trilobites from Scandinavia constitute at least 18 species representing four or possibly five genera. They are dominated by species of the genera Ellipsocephalus, Stenuaeva, and Proampyx. Two species have questionably been referred to Comluella, and a single species from the drill core File Haidar on Gotland has tentatively been assigned to Strenuella. According to Landing and others (1980, p. 403), the ptychopariids Comluella and Strenuella have not been recorded from cratonic regions and these trilobites were regarded as outer shelf margin inhabitants. However, as noted above, species tentatively referred to the genera Comluella and Strenuella occur in the Lower Cambrian shelf deposits of Scandinavia. In Skåne, Comluella(?) scania has been recovered from coarse bioclastic limestones suggestive of moderate to high energy conditions. These sediments are interpreted as shallow-water deposits (de Marino, 1980).

Stenuaeva, with S. primaeva (Brøgger, 1879) as type, is a distinct genus characterized by deeply impressed dorsal furrows, a wide transverse furrow in front of the glabella and the ocular ridges, inflated fixigenae, and a tumid anterior border. The genus is indicative of an Early Cambrian age. Species of Stenuaeva appear to characterize the Holmia kjerulfi Zone of Scandinavia. However, the genus is locally abundant in but not restricted to this zone, as it occurs also in the next zone above in Skåne according to Bergström and Ahlberg (1981). Outside Scandinavia, Stenuaeva has hitherto been recorded from Poland, Spain, and Morocco. One species, S. groenlandica (Poulsen, 1927), has been reported from northwest Greenland. However, I do not consider this species as a typical representative of Stenuaeva. The genus seems to have been a significant component in some of the faunas which inhabited the shelf areas of the eastern side of the Iapetus Ocean.

The Lower Cambrian ptychopariid trilobites of Scandinavia show their greatest affinity with ptychopariids described from Poland. Several closely related ellipsocephalid species are known from Poland, and the similarity in the faunas between the two areas indicates that they formed part of a single faunal

province, the Balto-Scandian Province in terms of Bergström (1976). The faunas of the Holmia kjerulfi Zone indicate a correlation with the Holmia Zone in Poland. The Proampyx linnarssoni Zone may be tentatively correlated with the Protolenus Zone in Poland (Bergström, this volume).

### DISTRIBUTION

Lower Cambrian ptychopariid trilobites are geographically widely distributed in Scandinavia. They have been recorded from a variety of localities along the Scandinavian Caledonides and in the Baltic Basin (fig. 1). Generally, the Scandinavian species

of the subfamily Ellipsocephaline have a limited regional extent. Moreover, they seem to be facies controlled. However, they may be useful for local correlations, as exemplified by Bergström and Ahlberg (1981) in the Lower Cambrian of Skåne.

A number of localities yielding ptychopariid trilobites are situated in the narrow belt of autochthonous sediments east of the Caledonian thrust front. However, several important localities are also known in the allochthonous sequence. Principal localities along the Scandinavian Caledonides are to be found in the Mjøsa area, southern Norway, and in the Laisvall and Torneträsk areas, northern Sweden. At Assjatj (Aistjakk), in the Laisvall area, a rich and well preserved Lower Cambrian fauna was described by Kautsky (1945). The fauna was obtained from the uppermost local Lower Cambrian (the top of the Grammajukku Formation). It is dominated by a ptychopariid trilobite, Ellipsocephalus gripi. Both larval and adult specimens occur in the collections of E. gripi. The associated faunal elements include a fallotaspid trilobite, Fallotaspis jungneri (see Bergström, 1973). At Mount Luopakke in the Torneträsk area, ptychopariid trilobites have been described both from the autochthonous sedimentary sequence and from the lowermost thrust nappe (Ahlberg, 1979, 1980). The largely carbonate restricted trilobite faunas of the Torneträsk area are provisionally assigned to the Holmia kjerulfi Zone. In northern Jämtland, an undetermined ptychopariid is associated with Calodiscus lobatus (Larsson, 1976).

In the Lower Cambrian of Skåne, southern Sweden, a thin but lithologically variable unit rests disconformably on a predominantly quartzarenitic sequence. This unit, forming the top of the local Lower Cambrian, has been distinguished as the Gislöv Formation (Bergström and Ahlberg 1981). Ptychopariid trilobites are abundantly represented in the Gislöv Formation. The species obtained are shown in figure 2. The lower part of the formation has yielded trilobites indicative of the Holmia kjerulfi Zone. Excluding ptychopariids, they include Holmia sulcata and Calodiscus lobatus?. Younger assemblages from the upper part of the Gislöv Formation are assigned to the Proampyx linnarssoni Zone. The topmost beds of the Gislöv Formation have yielded Ellipsocephalus lunatus and Comluella(?) scanica.

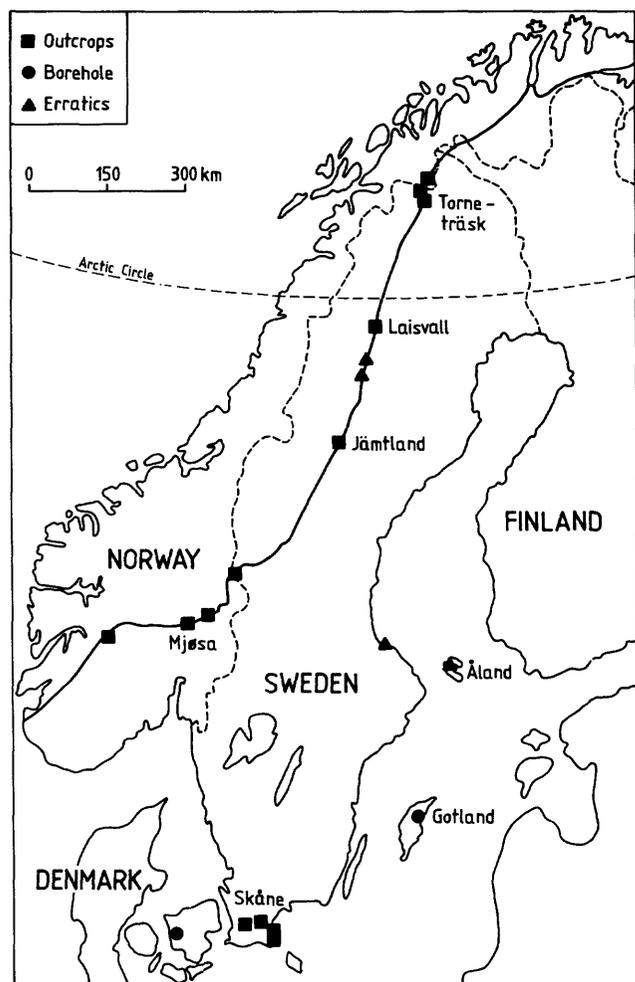


Figure 1.--Locations of sites that have yielded Lower Cambrian ptychopariid trilobites. The heavy line indicates the approximate position of the Caledonian thrust front.

SPECIES	AREA and ZONE		SOUTHERN SWEDEN		SOUTHERN NORWAY		LAISVALL AREA	TORNETRÅSK AREA	SEALAND, DENMARK
			Skåne (Gislöv Fm)		Mjøsa area		(Grammajukka Fm)	(upper shale fm)	(Slagelse No.1 Borehole)
	1	2	1	2	1	1?	1		
<i>Ellipsocephalus gripi</i>			□	□	■	□			
<i>E. nordenskiöldi</i>	■								
<i>E. lunatus</i>		■							
<i>Strenuaeva primaeva</i>			■						
<i>S. inflata</i>							■		
<i>S. spinosa</i>						■			
<i>S. ? kullingi</i>						■			
<i>S. n. sp.</i>		■							
<i>Proampyx rotundatus</i>	■								
<i>P. grandis</i>	■								
<i>P. sularpensis</i>	■								
<i>P. linnarssoni</i>		□		■					
<i>P. triangularis</i>							■		
<i>P. ? conifrons</i>								■	
<i>Comluella ? scanica</i>		■							
<i>C. ? lapponica</i>							■		

Figure 2.--Stratigraphic and geographic distribution of selected ptychopariid trilobites in the Lower Cambrian of Scandinavia. 1, *Holmia kjerulfi* Zone; 2, *Proampyx linnarssoni* Zone. Open squares represent either specimens questionably referred to the species or those referred to as cf.

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### 3. GENERALIZATIONS ABOUT GRAND CYCLES

By

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#### ESSENTIAL CHARACTERISTICS

A prominent feature of the Cambrian stratigraphy of the southern Rocky Mountains of Canada is the alternation of shaly formations with formations consisting entirely of carbonate rocks. Aitken (1966) first interpreted this alternation in terms of depositional cycles. I called these large-scale cycles ("300 to 2,000 feet thick, and spanning two or more fossil zones") grand cycles, to distinguish them from the meter-scale, shallowing-upward cycles common in the Cambrian platform formations I studied and in platform carbonates worldwide.

Several authors subsequently found division of the Cambrian column into "grand cycles" to be useful in Canada and elsewhere, not only as a descriptive, but also as an analytical device, because it was obvious from the beginning that these cycles at least approximate chronostratigraphic units.

Palmer and Halley (1979) used the concept of grand cycles as the basic framework for their analysis of the Carrara Formation of the southern Great Basin. They have given the most detailed description yet of grand cycles; it is one that fits in almost every detail the Middle Cambrian (Albertan Series) grand cycles of the Canadian Rockies, as redescribed by Aitken (1978).

Although no one has stated it in print, it is apparent that the Middle Cambrian, at least, of the southern Appalachians also is a stack of grand cycles with relationships similar, if not identical, to those described for the Rocky Mountains and the Great Basin (see Palmer, 1971, fig. 13). The question of synchronicity of these cycles in separate "basins" or geoclinal areas arose naturally (see A. R. Palmer, this volume).

The purpose of this brief paper is to:

- a. Describe the essential characteristics of grand cycles generally, as distinct from the details, and
- b. Consider, in particular, the nature of grand cycle boundaries: Are they disconformities? Are they isochronous surfaces (as judged by physical evidence)? Are they correlatable between "basins"?

Because all interpretations offered to date suggest grand cycles depend on continuous or nearly continuous subsidence for their development, and because these cycles are characteristic of miogeoclinal successions, they must be features of passive continental margins. They developed when early, rapid, post rifting, clastic deposition had slowed sufficiently to permit intermittent deposition of carbonate sediments on subsiding shelves, and they continued to develop until the supply of detritus had diminished sufficiently to permit continuous sedimentation of carbonate rocks. As seen through an overlay of distracting sedimentological detail, their essential characteristics are the following:

- a. The base is marked by the abrupt appearance of terrigenous mudrocks above a thick unit of carbonate strata. These basal mudrocks are the initial deposits of the shaly half-cycle.
- b. The shaly half-cycle consists of mudrocks interbedded with limestones and (or) sandstones. In the Carrara cycles, sandstones are prominent; in the Canadian Rockies, sandstone is rare, and beds of a variety of limestones (lime mudstone, grainstone, algal boundstone, etc.) are prominent. In the shaly half-cycle, either mudrocks or carbonate rocks may dominate. Meter-scale cyclicity (shallowing-upward, "clearing-upward" cycles) is widespread.
- c. The midpoint of the cycle is marked by the disappearance of mudrocks, at a gradational, interbedded contact between the shaly and carbonate half-cycles. This contact is diachronous, younger toward the craton.
- d. The carbonate half-cycle consists of various kinds of limestone and dolomitized equivalents, including lime-mudstone, grainstone, and cryptalgal boundstone. Minor amounts of clay, silt, and quartz sand may or may not be incorporated. Meter-scale, shallowing-upward cycles may or may not be apparent.
- e. The cycle ends with the abrupt reappearance of terrigenous mudrocks, the beginning of the next cycle.

Cratonward, typical grand cycles are recognized only to the pinchout of the carbonate lithosome (carbonate half-cycle), although in favorable circumstances, equivalent strata have been identified between marker beds in wholly clastic facies (Pugh, 1971).

Basinward, many grand cycles disappear as the shaly lithosome pinches out between carbonate lithosomes (fig. 2). Beds equivalent to the initial deposits of the cycle, have not been identified within the multi-story carbonate lithosomes of the outer platform, but such identification may not be impossible. In some cycles the shaly half-cycle is continuous with shaly basinal deposits seaward of the carbonate platform.

One of the necessary, though loosely defined, characteristics of grand cycles is scale. The ubiquitous, meter-scale, shallowing-upward cycles are not grand cycles. Neither are the kilometer-scale, unconformity-bounded sedimentary cycles (for example, Weller, 1960, p. 379; Gignoux, 1955, p. 18) of classical stratigraphy. Aitken (1966) put the scale at "300 to 2,000 feet of strata and two or more fossil zones," but this definition now requires modification.

The somewhat arbitrary nature of the distinctions between grand cycles and lesser cycles is illustrated by Aitken's (1966) identification of the cycle comprising the Mount Whyte and Cathedral Formations (580 m) as a single grand cycle (fig. 1). Had his work followed that of Palmer and Halley (1979), he probably would have seen the same succession as three cycles, the first beginning with the Mount Whyte, the second with the Ross Lake Shale Member, and the third with the upper shale member of the Cathedral. These smaller cycles would then correspond in scale (and in fauna) with the grand cycles of the Carrara Formation of the Great Basin. Nevertheless, no subdivision into yet smaller cycles would be reasonable, nor would any interval larger than the Mount Whyte-Cathedral cycle have any sort of unity in cyclical terms.

When the Mount Whyte-Cathedral cycle is divided into three grand cycles, the first cycle comprises the Plagiura-'Poliella' Zone, the second, the Albertella Zone, and the third, three quarters of the Glossopleura Zone. Another grand cycle that spans beds showing very little faunal change is the Pika Formation (390 m), comprising most, but not all, of the Bolaspidella Zone (Aitken, Fritz, and Norford, 1972). At the opposite extreme, the Sullivan-Lyell Grand Cycle (720 m) comprises most of the Cedarria Zone and all of the Crepicephalus and Aphelaspis Zones, while the Survey Peak Formation (520 m) comprises the top of the Saukia Zone and Zones A through G1 of the Lower Ordovician (Aitken and Norford, 1967). There is, thus, at least an order-of-magnitude correspondence in scale among these grand cycles, a unity seen again in a comparison of grand cycles in the

Canadian Rockies, the Great Basin, and the southern Appalachians (fig. 2).

Aitken's (1978) re-analysis of grand cycles in the Canadian Rockies emphasized the role of a platform-edge, peritidal rim. There, in every Middle and Upper Cambrian cycle for which the appropriate rocks are accessible, the deposits of such a rim are demonstrably present throughout the carbonate lithosome. In the interpretation of Palmer and Halley (1979), the rim appears only toward the end of the cycle and plays only a secondary role in its evolution. Palmer and Halley acknowledged, however (1979, p. 53) that they had not seen the transition from platformal to basinal facies, and by inference, that they had not seen the outermost platform deposits, precisely the expected locus of a rim.

#### Depositional Environments and Products

The foregoing paragraphs summarize the essential characteristics of grand cycles that can be perceived amongst a collection of extremely varied rocks, the products of depositional environments that are by no means the same from cycle to cycle.

The Lower and Middle Cambrian cycles of the Carrara Formation (Palmer and Halley, 1979) and the Albertan (Middle Cambrian) cycles of the Canadian Rockies (Aitken, 1966, 1978) are virtually identical. A peritidal, platform-rim facies passes cratonward into subtidal lime mudstones. The lime mudstones pass eastward into terrigenous mudrocks that apparently were deposited in water of similar depth and similarly low turbulence. The near identity of the Albertan and Carrara cycles extends to details, such as the abundance of oncoids in the lime mudstones near underlying shales and the eastward extension of a thin unit of cryptalgal laminite as the terminal event of the cycle.

In contrast to the consistency just described, the latest Early Cambrian Peyto Formation of Canada, a carbonate half-cycle overlying a sandstone-dominated half-cycle, is mainly of "high-energy" origin and is largely composed of coarse skeletal and ooid grainstone and oncoid packstone with large thrombolites at many localities. The coeval Gold Ace Limestone Member of the Carrara, on the other hand, is similar in every respect to the Middle Cambrian grand cycles overlying it.

The Pika Formation of the Canadian Rockies conforms to the stereotype of the Albertan grand cycles in the outer and inner parts of the platform. Along the mountain front, however, it contains at its top a long, narrow lens or member in which dolomitized, cyclically recurring beds of oolite and flat-pebble conglomerate are prominent (Aitken, in press). This member has no known counterpart in any other grand cycle; it appears to be localized above a

AGE	FORMATION	THKNS. (MAX)	LITHOLOGY	FOSSIL ZONES, FOSSILS
DRESBACHIAN	WATERFOWL	550' (165 M)	LIMESTONE, DOLOMITE	<u>CEDARIA</u>
?	ARCTOMYS	750' (228 M)	RED SHALE, SILTSTONE, DOL.	<u>BOLASPIDELLA</u>
MIDDLE CAMBRIAN	PIKA	900' (273 M)	LIMESTONE, DOLOMITE, SHALES NEAR BASE	<u>BATHYRISCUS</u> <u>ELRATHINA</u>
	ELDON	1100' (333 M)	LIMESTONE, DOLOMITE	<u>GLOSSOPLEURA</u>
	STEPHEN	450' (137 M)	LIMESTONE, SHALE	<u>ALBERTELLA</u>
	CATHEDRAL	1200' (364 M)	LIMESTONE, DOLOMITE	<u>PLAGIURA - POLIELLA</u>
	MT. WHYTE	450' (137 M)	LIMESTONE, STSTN., SHALE	<u>BONNIA - OLENELLUS</u>
LOWER CAMBRIAN	GOG GROUP	7,000' (2133 M)	QUARTZITE, MINOR SHALE	<u>NEVADELLA</u> <u>FALLOTASPIS</u>
	MURAL		LIMESTONE	UNNAMED
PRECAMBRIAN (WINDERMERE)	MIETTE GROUP	6,000' (1830 M)	SLATE, PEBBLE CGL., GRITS	NONE KNOWN EXCEPT RARE STROMATOLITES
	"HECTOR"		LS, PURPLE SLATE	
	"CORRAL CREEK"		SLATE, QTZ. - PEBBLE CGL., PEBBLY GRITS	

Figure 1.--Lower and Middle Cambrian stratigraphy, southern Rocky Mountains, Canada.

nascent structural high that later, in the Early and Middle Devonian, became more pronounced and emergent.

The Sullivan-Lyell cycle of Canada (fig. 3) shares only the essential characteristics of the Albertan grand cycles. In it, the platform-edge peritidal complex expanded enormously, as the Lyell Formation. The complex consists of a fringing belt of oolite with thrombolites, offlapping the strata of the shaly half-cycle and itself offlapped by strongly cyclical rocks of the shaly half-cycle (Sullivan Formation) accumulated in an inshore basin to the east that was separated from the open sea by the peritidal complex. Aitken (in press) concluded that these rocks-shales interrupted by spaced, massive beds of oolitic, skeletal and conglomeratic limestone--accumulated below wave base and that the ooids were introduced into the basin by mass-transport mechanisms from their site of origin, namely, the edge of the carbonate complex. Markello and Read (1981) have

independently arrived at a similar model for the deposition of the Nolichucky Shale of the southern Appalachians, which is at least partly coeval.

Finally, the most aberrant grand cycle known to me is that of the Arctomys (shaly) and Waterfowl (carbonate) Formations, straddling the Middle Cambrian-Upper Cambrian boundary (fig. 3). The carbonate half-cycle in this example resembles the Lyell Formation, described above, but the shaly half-cycle consists largely of peritidal, mudcracked red beds in shallowing-upward, meter-scale cycles. Salt hoppers, vuggy siltstone beds, and thin solution breccias are evidence of an evaporitic environment. The presence of sandstone beds in this cycle and the location of its pinchout, which is inferred to be far to the southwest of those of other Cambrian Grand Cycles, show that this cycle was deposited during a basinward stand of the shoreline. An episode of aridity (probably the one recorded by the Saline River evaporites of the Mackenzie Mountains) undoubtedly contributed to sediment character in this case.

## BOUNDARIES

Any geologist giving serious thought to the nature of grand cycles soon arrives at three questions about their boundaries:

- a. Are they disconformities?
- b. Are they isochronous?
- c. Can they be correlated extrabasinally?

These questions are approached in the context of formations with which I am most familiar.

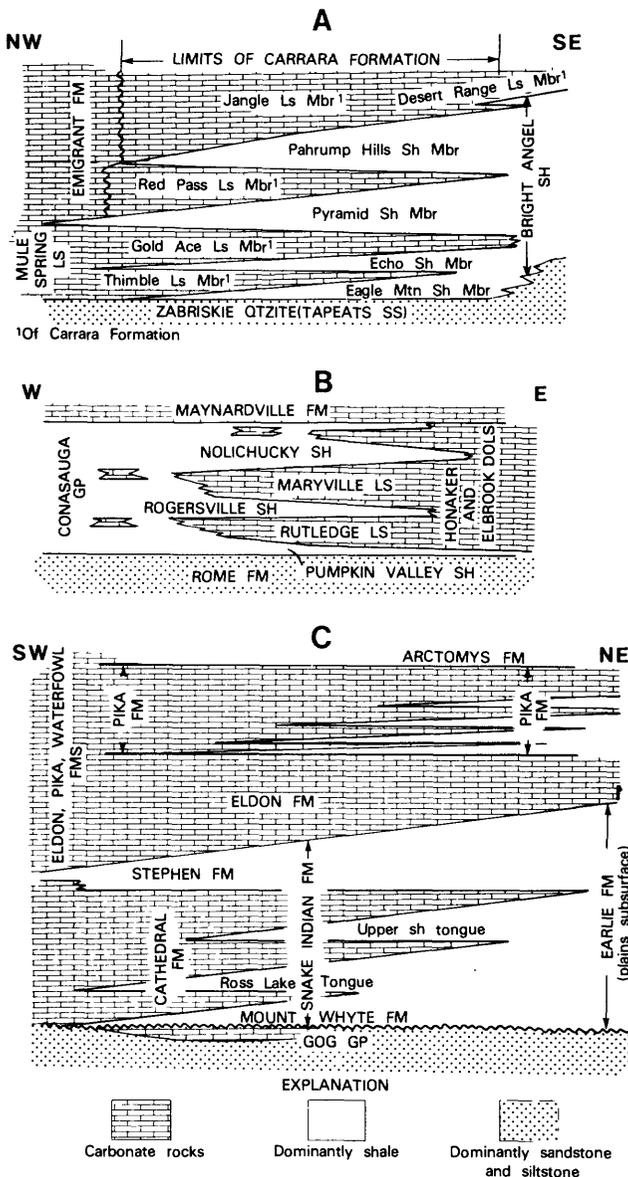


Figure 2.--Comparison of Grand Cycles in the southern Great Basin (top), the southern Appalachians (middle), and the southern Canadian Rockies (bottom). The panels are drawn at similar but not identical scales.

**Relation to Disconformities:** The answer to the question about disconformities may depend on position within a basin or, more properly, a geocline. In the thick, western sections of the Canadian Rockies, the base of the Survey Peak Grand Cycle is almost certainly conformable; the change from latest Cambrian to earliest Ordovician faunas takes place within the widely recognized basal silty member. At the base of at least one of the thinner, eastern sections, however, quartz sandstone unknown elsewhere fills erosional channels.

The Sullivan-Lyell Grand Cycle has a clearly marked basal contact in the thick western sections, but has not been shown to be disconformable. Again, however, unequivocal erosional relief has been observed at an eastern section and, in the subsurface of the Plains, the Sullivan oversteps the entire Arctomys-Waterfowl Grand Cycle, to lie unconformably on the Pika.

On the other hand, the Cathedral-Stephen and Eldon-Pika contacts are gradational, as are the contacts at the bases of shaly members in the Cathedral Formation, viewed as grand cycle boundaries. I would guess that the boundaries of grand cycles are, as a rule, conformable in thick, basinward sections, but that most or all of them may pass into disconformities toward the craton.

**Relation to Isochronous Surfaces:** Aitken (1966) gave evidence suggesting that the bases of grand cycles approximate isochronous surfaces. (Some of the faunal evidence cited then now requires revision.) These suggestions can now be supplemented.

As discussed earlier, the Mount Whyte-Cathedral cycle can be treated as three grand cycles, rather than one, to achieve harmony with the Palmer-Halley treatment of cycles in the Carrara Formation. In the southern half of the region studied by Aitken (1966, 1978), the upper and Ross Lake Members of the Cathedral Formation are very thin, only one or two meters, and they are shaly half-cycles. In view of the self-evident rule that "time planes do not cross tongues," these thin members approximate isochronous surfaces. Detailed lithostratigraphic and biostratigraphic correlations (Aitken, in press) demonstrate that the northeastward thickening of these members is at the expense of the overlying carbonate half-cycle; therefore, even where the tongues have thickened to tens of meters, their bases are probably isochronous.

In an astonishingly belated discovery of the obvious, Aitken (in press) realized that over a region of at least 20,000 km<sup>2</sup>, the lower member of the Stephen Formation, long recognized by him informally and now formalized in manuscript, consisted of two, and only two, small-scale shallowing-upward, "clearing-upward" cycles dominated by subtidal lime mudstone. Except at the platform-edge rim, these cycles do not contain peritidal facies (fig. 4); hence, they are not subject to

AGE	FORMATION	THKNSS. (MAX)	LITHOLOGY	FOSSIL ZONES, FOSSILS
ORDOVICIAN	SURVEY PEAK			
TREMPEA-LEAUAN	MISTAYA	500' (152 M)	LIMESTONE, DOLOMITE, STROMATOLITES PROMINENT	<u>SAUKIA</u>
	BISON CREEK	700'	SHALE, LIMESTONE	<u>PTYCHASPIS-PROSAUKIA</u> <u>CONASPIS</u>
FRANCONIAN	LYELL	1200' (370 M)	LIMESTONE AND DOLOMITE, CYCLIC; SANDY, SILTY, AND CHERTY ZONES	<u>ELVINIA</u> <u>DUNDERBERGIA</u>
DRESBACHIAN	SULLIVAN	1400' (431 M)	SHALE, LIMESTONE	<u>APHELASPIS</u> <u>CREPICEPHALUS</u>
	WATERFOWL	675' (208 M)	LIMESTONE, DOLOMITE, SILTSTONE	<u>CEDARIA</u>
	ARCTOMYS	775' (237 M)	INTERBEDDED RED AND GREEN SHALES AND SILTSTONES; MINOR LIMESTONE AND DOLOMITE; SALT-HOPPERS	<u>BOLASPIDELLA</u>
MIDDLE CAMBRIAN	PIKA			

Figure 3.--Upper Cambrian stratigraphy, southern Rocky Mountains, Canada.

interpretation as diachronous, progradational cycles. The conclusion that each of the cycles is isochronous, and that the top of the Cathedral Formation, upon which the lower cycle rests, is also isochronous, seems inescapable. Faunal evidence agrees: Glossopleura has not been found above the lower member of the Stephen, nor trilobites of the Bathyriscus-Elrathina Zone below the upper member.

The model presented by Palmer and Halley (1979, p. 54; fig. 34) for the Carrara Formation shows slight diachroneity at the bases of grand cycles. Diachroneity in this case is not supported by faunal or physical evidence but is a necessary corollary of the hypothesis adopted to explain the cycles. Given the virtual identity of the Carrara and Albertan cycles, it appears fair to challenge the Palmer-Halley interpretation with evidence from the lower Stephen Formation, given above.

Apparent diachroneity of grand cycle boundaries that might seemingly be supported by faunal evidence

is illustrated by relations between the Cathedral and Stephen Formations near Kicking Horse Pass on the Alberta-British Columbia border. There, each of the two lime-mudstone dominated, small-scale cycles forming the lower member of the Stephen (see above) is traced westward into platform-rim facies; the basal shale pinches out, and the lime mudstones change largely to cryptalgal laminite (fig. 4). Over the axis of the platform rim, these strata are coarsely dolomitized and have properly been considered to belong to the top of the Cathedral Formation, but the two cycles of the lower Stephen can still be recognized. In the same area, a Bathyriscus-Elrathina fauna appears with the shales of the upper member. If these fossils are taken to be "basal Stephen," they support diachroneity (for example, Fritz, 1971). The anomaly is a peculiarity of the platform rim and must not be given regional significance.

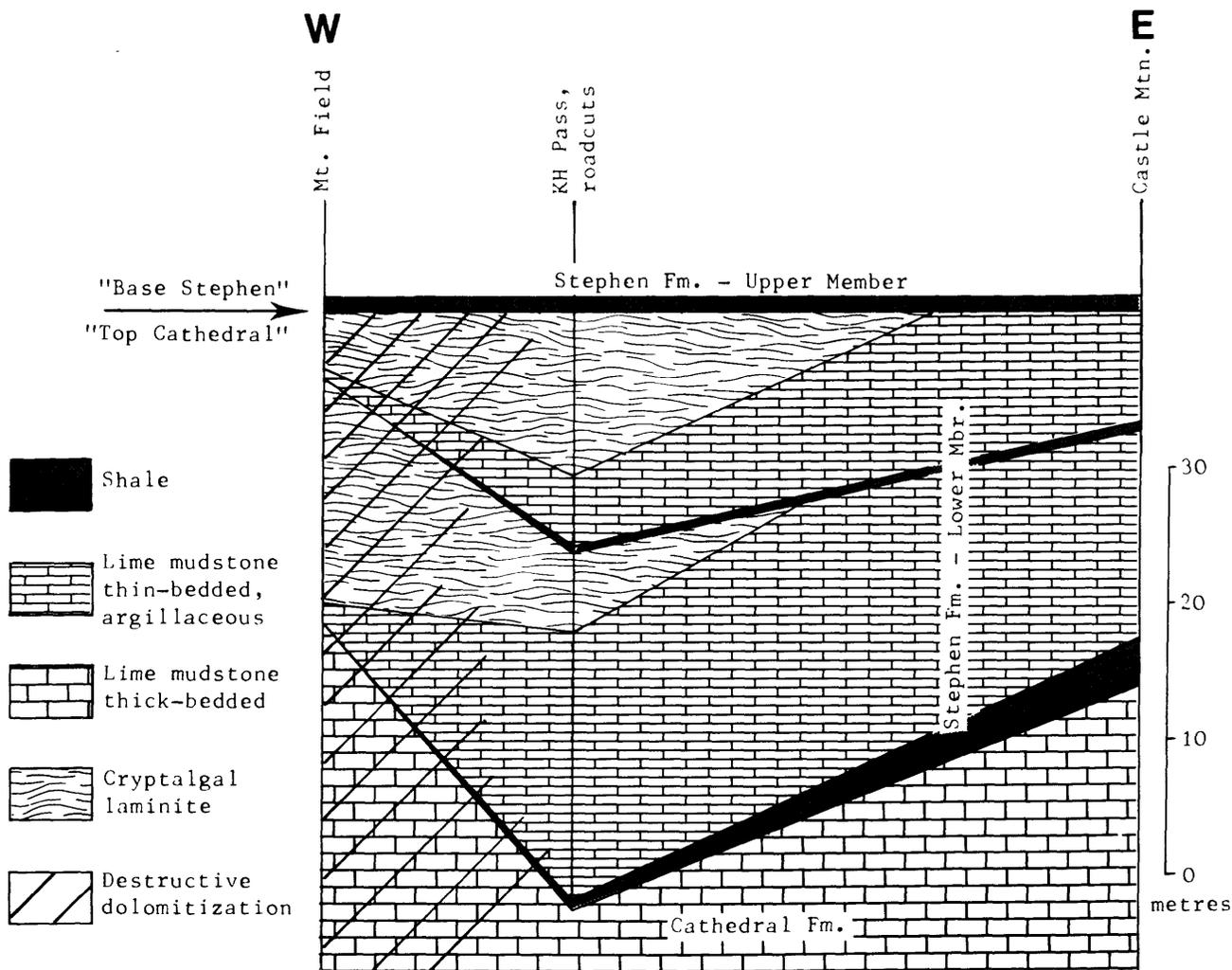


Figure 4.--Stratigraphic cross sections of the lower member of the Stephen Formation from inshore basin (E) to "rim" (W) facies, along Highway No. 1, Alberta and British Columbia.

Correlation of Grand Cycles: The question of the "interbasinal" correlation of grand cycles is perhaps the matter in which the study of cycles can make important contributions toward broader questions, such as the history of sea level. A. R. Palmer (this volume) addresses this question in detail.

Given that grand cycles are phenomena of passive margins, and that such margins are known to subside continuously at an exponentially decreasing rate (Sleep, 1971, 1976), the observed cyclicity must be related to changes in either the direction or rate of eustatic sea-level change (Pitman, 1978). If biostratigraphy can distinguish consistently between successive grand cycles, we could then be confident that in correlating grand cycle boundaries, we are correlating events in sea-level history and identifying the isochronous surfaces that are so rare and so valuable in the interpretation of stratigraphy.

In searching, in a preliminary way, for correlations between the southern Canadian Rockies and the southern Appalachians (as summarized by Palmer, 1971, p. 200-204), one seizes immediately on the following correlation of grand cycles (see fig. 2):

Canadian Rockies	Southern Appalachians
Pika	Cycle above Maryville Fm.
Stephen-Eldon	Rogersville-Maryville
Mount Whyte-Cathedral	Pumpkin Valley-Rutledge

These correlations are imperfect on the basis of published data. I suggest that a reexamination of the Appalachian succession, oriented along the lines of grand cycle analysis, might prove the cycles to be in perfect synchrony, within the resolving power of biostratigraphy. There are striking parallels, even in

style, between the grand cycles of the two regions. The Appalachian Middle Cambrian cycles, like those in the West, have carbonate lithosomes that are limestone toward the craton and dolomite toward the platform edge. In both regions, the overlying, thick, Upper Cambrian carbonate lithosome (Conococheague Group and Copper Ridge Dolomite in the Appalachians, Lynx Group in Alberta) shows the reverse arrangement, with dolomite landward and limestone seaward. Coincidence falls as a plausible explanation for these parallels; I conclude that they are a common response, on opposite sides of the craton, to sea-level behavior.

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#### 4. THE CAMBRIAN-ORDOVICIAN BOUNDARY IN THE MALYI KARATAU RANGE SOUTH KAZAKHSTAN

By

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A continuous carbonate section from the Upper Cambrian (Lisogor, 1977; Ergaliev, 1981) up to the Arenigian Stage crops out along the Batyrbai Dry Creek in the Malyi Karatau Range, South Kazakhstan (Chugaeva and Apollonov, 1981). The section spans all the three possible locations for the Cambrian-Ordovician boundary: (1) the base, (2) the middle, and (3) the top of the Tremadocian Series (Henningsmoen, 1973; Chugaeva, 1976). Of the three possible horizons the most widely used is that at or near the base of the Tremadocian Series, and it is this alternative that we accept herein. Therefore, we consider here only the lower part (approximately 300 m) of the section adjacent to the boundary under consideration. Measurements of the section and identification of the trilobites collected were made by M.A. Apollonov and M.N. Chugaeva; conodonts were identified by S.V. Dubinina.

The part of the Batyrbai section under consideration consists of dark (almost black), flaggy, fine-grained limestones interbedded with lighter colored calcarenites and flat-pebble carbonate breccias, some of which have inclusions of white Epiphyton-bearing limestones. These dark-colored deposits seem to have formed under relatively deep-water environments on the open shelf, while the light-colored rocks are presumably of slump-breccia origin. The dark-colored limestones are especially fossiliferous. Trilobites and conodonts were sampled from the same layers.

#### BIOSTRATIGRAPHY AND CORRELATION

Ranges of the main trilobite and conodont taxa in the Batyrbai section and its correlation with stratigraphic sequences of some other regions are shown on figure 1. Some comments concerning this figure follow:

1. A number of biostratigraphically defined units have been established in the section. The lower boundary of each of them is defined by the appearance of new elements in conodont and (or) trilobite associations.

2. The two agnostid zones in the Hedinaspis-bearing beds are established in a nearby section (Ergaliev, 1981) and traced into the present section.

3. The durations of the various trilobite and conodont associations prove to be different in successive parts of the section: a single conodont association (Westergaardodina, Furnishina, Proconodontus, Prooneotodus) characterizes that part of the section below the base of the Harpidooides-Platypeltoides beds, which is separated into two (or three) trilobite subdivisions. On the other hand, the Euloma-Leiostegium beds incorporate three successive conodont assemblages, (III) Cordylodus proavus, (IV) C. oklahomensis, and (V) C. lindstromi.

4. Worthy of attention is the remarkable coincidence of trilobite and conodont associations at some levels: (a) the association of Proconodontus notchpeakensis, P. muelleri, P. carinatus, Oneotodus nakamurai, and O. gracilis appears at the base of the Harpidooides-Platypeltoides beds; (b) Cordylodus proavus occurs just at the base of the Euloma-Leiostegium beds; and (c) the appearance of the C. prion coincides with the base of Dikelokephalina beds.

5. The trilobite association of Hedinaspis, Plicatolina, Charchagia, and abundant agnostids is easily traced in the Zolotokitkat Horizon of the Altay-Sayany region of southern Siberia (Petrunina, 1967), in southern China (Lu Yanhao, 1980), and in the uppermost part of the Franconian Stage in central Nevada, U.S.A. (Taylor, 1976); some elements of the fauna are also known from the Franconian II of Alaska (Palmer, 1968). These occurrences suggest the correlation of the above-named beds.

6. The Lophosaukia beds and the Harpidooides-Platypeltoides beds together seem to correlate with the Trempealeauan Stage of North America (except its uppermost part, the Corbinia aopsis Subzone) (Palmer, 1979), as these beds contain of Saukiidae, Eurekiidae and Richardsonellidae.

The presence of Lophosaukia, Koldinioidia, and Ivshinaspis (similar to Mendosina) connects the faunas of these horizons with the Payntonian Stage of Australia, where the sauikiids are most diverse, as in our section. The occurrence of the Proconodontus notchpeakensis association in the Harpidooides-Platypeltoides beds supports such correlation.

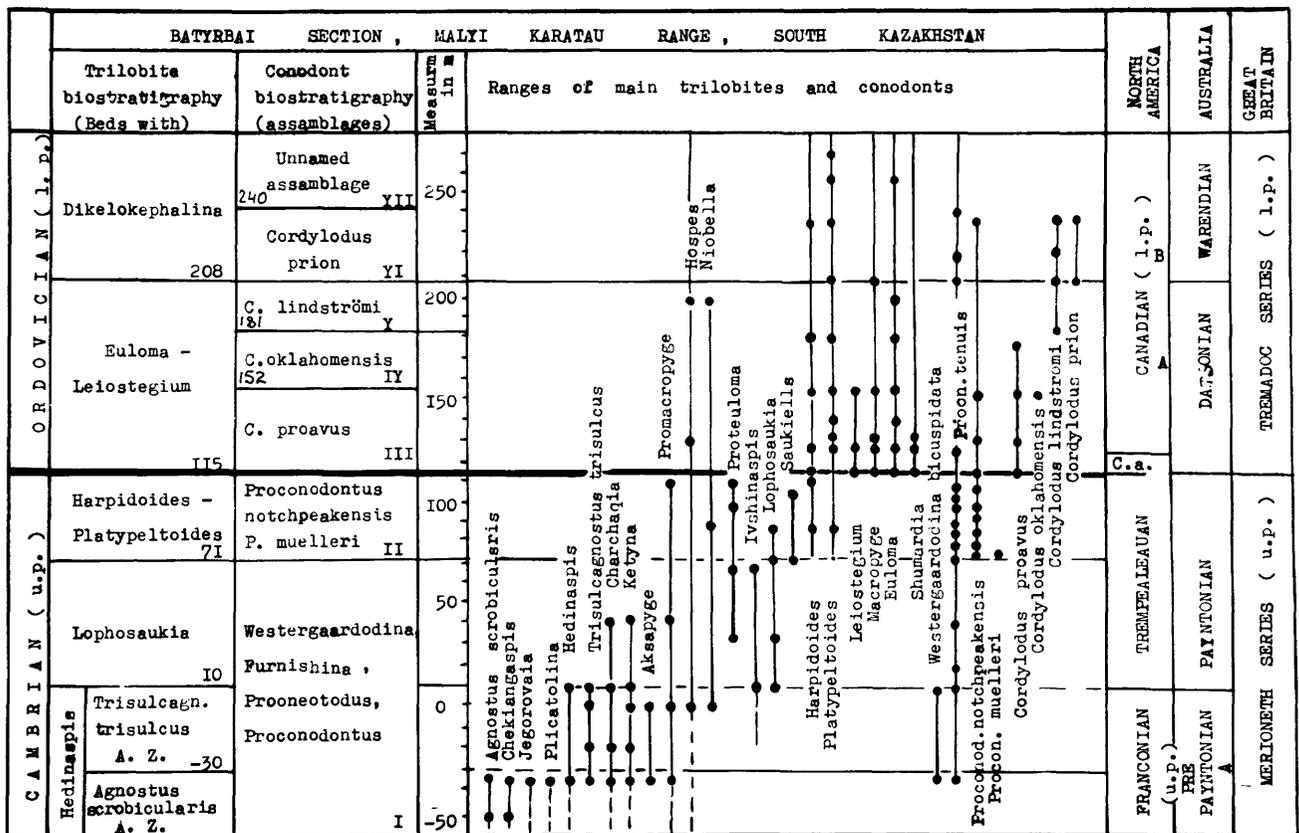


Figure 1.--Biostratigraphy and correlation of the Uppermost Cambrian and Lowermost Ordovician of the Batyrbai section. The heavy horizontal line is the suggested Cambrian-Ordovician boundary. Abbreviations: A.Z. = Assemblage Zone; l.p. = lower part; u.p. = upper part; C.a. = Corbinia apopsis Subzone of Saukia Zone in North America. Solid circles denote reported occurrences of the taxa.

7. The Euloma-Leiostegium beds contain some taxa similar to British early Tremadocian trilobites (Macropyge cf. M. chermi, Shumardia cf. S. curta, Euloma cf. E. monile). This suggests the correlation of the beds with the lower Tremadocian Series.

The trilobite-based correlation of the Euloma-Leiostegium beds with North American and Australian sections is nearly impossible. Trilobites of this level in North America are very different from Kazakhstania forms and are represented by a few genera of the "hystricurid" biotaxa (Stitt, 1975), and trilobites of this level are very rare in Australia.

Nevertheless, the correlation of Euloma-Leiostegium beds with the carbonate sections of Australia and North America is reliably supported by conodonts, by the appearance of the Cordylodus proavus association, which marks the base of the Corbinia apopsis Subzone in North America and the base of the Datsonian Stage in Australia (Jones, and others, 1971). The evolutionary succession of conodonts (Proconodontus notchpeakensis to Cordylodus proavus) is very similar in the carbonate sections of Asia, Australia, and North America.

From the trilobite and conodont data it seems likely that the base of the lower Tremadocian approximately coincides with the base of the Corbinia apopsis Subzone in North America and with the base of the Datsonian Stage in Australia.

In spite of some differences in points of view on the interprovincial correlation of this level (Landing, and others, 1978; Fortey and Skevington, 1980), the divergence of opinions on the location of the system boundary does not exceed significantly the resolving power of the biostratigraphic methods.

8. Some trilobites appearing in the Dikelokephalina beds (Dikelokephalina, Harpides, Symphysurus) are characteristic of the European upper Tremadoc. This suggests a late Tremadocian age for these beds but does not prove exact coincidence of their lower boundary with the European Upper Tremadoc. Correlation with the Australian and North American sections is based on conodonts, specifically on the appearance of Cordylodus prion.

## Characteristic Features of the Batyrbai Section Fauna

A. The trilobite assemblages have very few endemic genera.

B. The specific composition and the evolutionary succession of the conodont assemblages nearly duplicate those in the Australian and North American sections.

C. The uppermost Cambrian trilobites appearing below the base of the Euloma-Leiostegium and Cordylodus proavus beds have some "Pacific" elements, whereas trilobites above this level have more in common with those of the "Atlantic" Province.

D. Two distinctive groups of trilobite taxa can be recognized. The first one is represented by a succession of morphogenetically related genera that have relatively long time ranges through the section. Late Cambrian representatives of this group seem to be ancestral for the Atlantic (non-olenid) fauna that is widespread in the European Lower Tremadoc. They were the origin of such "Atlantic" genera as Macropyge (the Aksapyge-Promacropyge-Macropyge stock), Euloma (Ketyna-Proteuloma-Euloma stock), Harpides (Harpidooides-Harpides), and Shumardia (Hospes, Koldinioidia, Shumardia). The other group is represented by relatively short-ranging genera, having neither ancestors nor descendants within the section. They are not typical of the "Atlantic" fauna, though some of them are known among the "Pacific" fauna. Saukiidae, Eurekiidae, and others (Hedinaspis, Charchaqia, Plicatolina) are found in the Sayan-Altay region of Southern Siberia and in deep-water deposits of central Nevada, U.S.A.

The conodont and trilobite fauna of the Bastyrbai section can serve as a connective link between the heteroprovincial faunas of Late Cambrian and Early Ordovician age and can help us to understand the origins of the European Tremadocian (non-olenid) trilobites. The Batyrbai section is totally exposed, continuous, abundantly fossiliferous, composed of monofacial rocks, and easily accessible; thus it satisfies the requirements imposed upon boundary stratotypes. Hence the section can be recommended as a candidate for the Cambrian-Ordovician boundary stratotype.

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## 5. THE SUCCESSION OF SKELETAL FOSSILS IN THE BASAL LOWER CAMBRIAN OF SOUTHEASTERN NEWFOUNDLAND

By

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Preliminary field investigations by Fletcher, involving new discoveries of fossiliferous horizons in continuous sedimentary sequences spanning the Precambrian-Cambrian transition on the Burin Peninsula, southeastern Newfoundland, prepared the ground for a visit to the area by a party of the Precambrian-Cambrian Boundary Working Group (IGCP Accession No. 29) in July 1979. On that trip (led by Fletcher), Bengtson sampled the sequences for an additional assessment of the stratigraphic potential of skeletal microfossils in the lowermost Cambrian beds, below the lowest known trilobite-bearing strata in the area. This report presents the combined results of the above mentioned studies.

Two major successive assemblages of biostratigraphic significance below the first trilobites can be recognized: a lower, Aldanella attleborensis Assemblage, also characterized by Heraultipegma n. sp. and Fomitchella cf. acinaciformis, and an upper, Coleoloides typicalis Assemblage. Both assemblages contain additional taxa of potential significance to correlation: hyoliths, gastropods(?), monoplacophorans(?), wiwaxiids, and (so far only in the C. typicalis Assemblage) lapworthellids, tommotiids, and other similar phosphatic fossils. In terms of the key successions of the Siberian Platform, the A. attleborensis assemblage is considered to represent the Tommotian Stage whereas the C. typicalis Assemblage, as recognized here, probably belongs to the lower Atdabanian Stage.

In the Bonavista-Avalon region, where the succession of formations in the Lower Cambrian consist of the Random and Bonavista Formations, the Smith Point Limestone, and the Brigus Formation, the A. attleborensis Assemblage is replaced by the C. typicalis Assemblage within the Bonavista Formation,

whereas the first trilobites (Callavia Zone) appear near the contact between the Smith Point Limestone and the Brigus Formation. The quartzitic Random Formation in this area rests with a marked disconformity on clastic rocks of the Musgravetown Group; its contact with the overlying Bonavista Formation is also disconformable. In the Grand Bank area at Fortune Bay on the Burin Peninsula, however, Random-type quartzites are conformably underlain by a thick sequence of sandstones, siltstones, and mudstones (with thin limestone bands) assigned to the Doten Cove and Chapel Island Formations. The Doten Cove which contains trace fossils, and the upper part of the Chapel Island Formation contains skeletal fossils of the A. attleborensis Assemblage. In the St. Lawrence area on the Burin Peninsula, part of the Chapel Island Formation and the whole Random Formation is missing; the Doten Cove Formation and the lower part of the Chapel Island Formation are directly overlain by a sequence of mudstones with thin intercalated limestone bands. In the mudstone sequence, a faunal shift from the A. attleborensis to the C. typicalis Assemblage is documented, thus the situation recalls that encountered in the Bonavista Formation elsewhere.

The Random Formation, where present, appears to have been deposited during the time marked by the A. attleborensis Assemblage. There is no conclusive biostratigraphic evidence for strong diachronism of this unit such as proposed by some previous investigators.

The Fortune Bay-Burin region offers good promise for further biostratigraphic studies of trace fossils and skeletal fossils within continuous sedimentary sequences representing the Precambrian-Cambrian transition.

## 6. COELOSCLERITOPHORA — A MAJOR GROUP OF ENIGMATIC CAMBRIAN METAZOANS

By

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The earliest skeletonized faunas of the Cambrian reflect a major metazoan radiation, which may have produced a number of short-lived taxa at or near the level of phyla. (For example, see Stanley 1976, p. 72). The faunas are characterized by a large proportion of forms of uncertain affinities (see review by Brasier, 1979, and references therein.) The perplexing variety of more or less strangely shaped skeletal elements in the Lower Cambrian is leading to a profusion of poorly defined systematic names, particularly at the levels of species and genus. This may be ascribed to our (1) lack of knowledge of the organization of the animals, (2) lack of appreciation of phenetic variation within populations, and (3) lack of understanding of the phylogenetic relationships among taxa. Clearly, a better understanding of the biology of these early skeletonized metazoans would improve the situation on all counts and would also shed light on the more general aspects of the early metazoan radiation.

We will discuss here a number of seemingly unrelated Cambrian fossils with the intent to demonstrate their probable derivation from a common ancestor near the beginning of the Cambrian. The animals are characterized by a composite exoskeleton, the individual sclerites of which have a prominent internal cavity and a restricted basal foramen. Currently named taxa include the families *Wiwaxiidae* Walcott 1911 (= *Halkieriidae* Poulsen 1967, = *Sachitidae* Meshkova 1969), *Siphogonuchitidae* Qian 1977, and *Chancelloriidae* Walcott 1920. Members of these taxa were abundant and widespread, particularly during the Early Cambrian, yet no post-Cambrian representatives are known. The suggestion of monophyletic derivation is based on the particular construction of the sclerites, which implies an unusual mode of secretion that is unlikely to have arisen independently in several metazoan lineages.

We are currently engaged in a detailed investigation of the structure, composition, and functional morphology of these various Cambrian fossils in order to assess the tenability of these ideas and to elucidate the biology, taxonomy, and affinities of the group. The following presentation summarizes the salient features of each family, stressing important similarities and differences between them.

### Family WIWAXIIDAE Walcott 1911

*Wiwaxia corrugata* is best known from the Middle Cambrian Burgess Shale, where well-preserved, nearly complete specimens have been found (Walcott, 1911). (The material is currently being restudied by Simon Conway Morris at Milton Keynes, England.) The animal was as much as a few centimeters long and covered with a mail armour of imbricating scales and projecting spines. *W. corrugata* was long considered to be without known close relatives, but comparisons of its dermal elements with those of the Lower Cambrian fossils known as *Halkieriidae* Poulsen 1967 (= *Sachitidae* Meshkova 1969) reveal close morphological and structural similarities. We refer all of these to the *Wiwaxiidae*.

*Wiwaxiid* sclerites commonly represent two basic types, flattened scales (fig. 1A), and spines with rounded transverse cross sections. There is usually a surface ornament of longitudinal ridges. The sclerites have a large internal cavity which opens through a smaller foramen at the base. The walls of the flat sclerites sometimes show a complex pustulose or tubular internal structure in their thicker, peripheral parts. Judging from their various modes of preservation, the Lower Cambrian representatives appear to have had a calcareous composition; however, there is no evidence of primary mineralization in the Burgess Shale *Wiwaxia* (S. Conway Morris, personal communication, 1978).

*Wiwaxiid* sclerites in the Lower Cambrian are almost always found dissociated, and their nature as components of a complex exoskeleton has not always been understood (for example, Poulsen, 1967). In the Lower Cambrian material available to us there is only one example of a small set of articulated sclerites.

### Family SIPHOGONUCHITIDAE Qian 1977

The *Siphogonuchitidae* are represented by elongate sclerites with polygonal transverse cross sections and a large internal cavity (fig. 1B). Only Lower Cambrian representatives are known.

There is a fairly prolific flora of published generic and specific names within this family, and some taxa have been included which may not belong there; the present discussion centers on forms with the

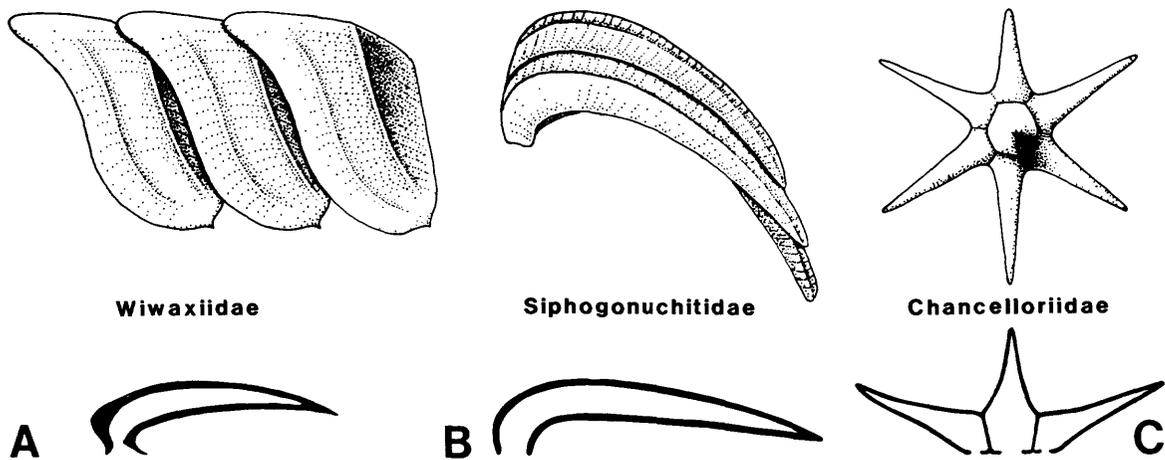


Figure 1.--Arrangement of sclerites (top) and longitudinal cross-sections of sclerites (bottom) in Wiwaxiidae (A, represented by Sachites sp.), Siphogonuchitidae (B, represented by Dabashanties? sp.), and Chancelloriidae (C, represented by Chancelloria sp.). Reconstructions based on evidence from natural associations. About x40.

above-mentioned characters, present in the type genus Siphogonuchites Qian 1977. Most published photographs of siphogonuchitids (for example, Qian, 1977; Qian, Chen, and Chen, 1979) show specimens that appear to be incomplete in the basal region, but well-preserved specimens from Lower Cambrian sections in Mongolia (material kindly made available for study by Nadezhda V. Grigor'eva, Moscow) show that they typically have a somewhat restricted, laterally deflected basal opening comparable with the ones found in wiwaxiids and chancelloriids. Some of the specimens from Mongolia are preserved as bundles of sclerites (fig. 1B), similar to the specimens shown by Chen (1979, pl. 1:2-3) as Dabashanites mirus. In these bundles, the individual sclerites cover each other in a complex pattern, and the longitudinal facettes (reflected in the polygonal cross sections) represent surfaces of contact.

Many siphogonuchitid sclerites are preserved with phosphatic walls; whether or not this was the original mineralogical composition is not known.

#### Family CHANCELLORIIDAE Walcott 1920

Chancelloria is known from nearly complete specimens in the Burgess Shale (Walcott, 1920). There is some doubt whether all the forms described by Walcott as Chancelloria represent the same kind of animal, but Goryanskiy's (1973) subsequent designation of the specimen illustrated by Walcott's (1920) plate 86, figure 2, as the lectotype for the type species, C. eros, establishes the genus as being characterized by the kind of sclerites discussed here. Chancelloriid sclerites are among the most common Lower Cambrian fossils and range into the Upper Cambrian. The

sclerities are composite; typically they are star-shaped and have a varying number of radiating spines and, usually, a central spine or knob (fig. 1C). Each ray of the star has a separate internal cavity which opens to the exterior through a smaller basal foramen; the walls are calcareous (Sdzuy, 1969). The surfaces having the basal foramina unite to form a distinct, flat basal surface of the composite spicule.

With few exceptions (for example, Goryanskiy, 1973), published discussions of the Chancelloriidae have presupposed a sponge affinity, mainly because of the specimens referred by Walcott to Chancelloria. However, sponge spicules are formed by enveloping sclerocytes and grow centrifugally, whereas in chancelloriid sclerites the presence of thin internal walls separating the cavities of the individual rays (Sdzuy, 1969) shows that the walls were secreted by the tissue occupying the cavities. These chancelloriid sclerites cannot be homologous to sponge spicules; instead, their structure and morphology suggest that they were dermal sclerites forming an external cover of protective spikes.

#### CONCLUSIONS

The mineralized sclerites of the groups discussed herein are all hollow and have a restricted basal opening to the outside. The shape of the basal region shows that the sclerites did not grow by simple successive accretion; the restricted foramen is present even in the smallest specimens, and larger specimens do not have similar earlier growth stages incorporated in their shape. Natural associations of sclerites are known in each group: the sclerities either formed a scaly armour (Wiwaxiidae) or were gathered in bundles

(Siphogonuchitidae) or star-shaped aggregates. Because the sclerites were often in contact with one another along snugly fitting surfaces (in the case of the Chancelloriidae they even have a common wall in the zone of contact), their probable mode of formation was by mineralization along the surfaces of organic precursors, which then came to occupy the internal cavities of the sclerites. The sclerites were thus external structures forming a more or less coherent armour. Growth of this exoskeleton took place either by the addition of new sclerites or by the replacement of smaller sclerites with larger ones. The fundamental similarities in skeletal organization between the discussed families indicate that this type of skeleton is a homologous feature which can be used to recognize a monophyletic group of high taxonomic rank. We propose the name *Coeloscleritophora* for this group, provisionally assigning it to class level.

We hope that the outline concepts of the class *Coeloscleritophora* will stimulate research into the biological nature of this large and enigmatic group of metazoans, and that increased attention to the complex nature of their skeletal armour will eventually resolve the currently growing conflict between form-taxonomy based on the shape of isolated sclerites (or even fragments of sclerites) and taxonomy based on biological interpretations.

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## 7. LOWER CAMBRIAN SHELLY FAUNAS AND BIOSTRATIGRAPHY IN SCANDINAVIA

By

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In several contributions A. H. Westergård (1922, 1942, 1946-48, 1950, 1953) described the Middle and Upper Cambrian stratigraphy and trilobite faunas of Sweden. Another major contribution was made by G. Henningsmoen (1957) on the Upper Cambrian of Norway. These and other contributions have made the Middle and Upper Cambrian of Scandinavia well known to Cambrian specialists all over the world, and the Middle Cambrian of Scandinavia has been used as a kind of standard succession for the Middle Cambrian.

The situation in the Lower Cambrian of Scandinavia is much different. On the whole, correlation is very difficult because many faunas only occur locally and because trilobites are poorly represented in many sections and areas. Although Lower Cambrian trilobites were first described from Scandinavia a century ago, their general rarity and poor preservation permitted only slow growth in our knowledge of them. Certain areas, such as the present Baltic are almost devoid of known trilobites, and authorities differ on the correlation between facies in different areas. Recently, however, a combined effort has been made to collect and describe trilobites, acritarchs and other fossils (P. Ahlberg, S. Bengtson, J. Bergström, S. Fjøn, G. Vidal, unpubl. data), and this effort has led to a new understanding of Lower Cambrian stratigraphy and correlation.

The transition between the Vendian and the Lower Cambrian is not known with certainty to be complete anywhere in Scandinavia. In the north (Lappland), there is an uppermost Vendian (Valdaian) association with vendotaenid algae, the medusoid Kullingia concentrica, and trace fossils. At Lake Torneträsk and in Troms, Norway, the overlying beds contain Platysolenites antiquissimus and, according to reports, also contain Volborthella tenuis. As Volborthella does not seem to occur elsewhere in strata below the Schmidtiellus mickwitzi Zone, and Platysolenites is not reported from strata above this zone, these overlying beds would seem to belong to this trilobite zone. However, Spirosolenites spiralis and Aldanella kunda, which are associated with Platysolenites and Volborthella in Lappland, also occur in the Lontova Clay in Estonia and so may indicate the Platysolenites antiquissimus Zone. Anyway, there seems to be a hiatus in the Lappland sequence corresponding to the Sabellidites cambriensis Zone and part of the Platysolenites antiquissimus Zone in Poland.

In southern Scandinavia the succession starts with quartz arenites: Kalmarsund Sandstone on the Baltic coast, Hardeberga Sandstone in Skåne (southernmost Sweden) and Bornholm, Ringsaker Quartzite Member in the Oslo area. Acritarchs (G. Vidal, unpubl. data) and trilobite traces indicate that much if not most of the Hardeberga Sandstone belongs to the middle part of the Lower Cambrian. There is nothing in the trace fossil fauna to indicate that any part of these arenites is notably older, and they may have been deposited during a fairly short time interval.

Above this level are basically an eastern biofacies and a western one. The eastern biofacies is characterized by the general lack of trilobites and by the presence of small shells such as Mobergella and Mickwitzia. In the western biofacies there are enough trilobites and other fossils to make a fairly reliable biostratigraphic subdivision. In the last few years it has become possible to make a rough correlation between the two facies.

### Schmidtiellus mickwitzi Zone

Although trilobite traces are present in the Hardeberga Sandstone (including Nexø and Balka Sandstones), the oldest known Scandinavian trilobite fauna is found in the overlying Norretorp Formation. The zone was known previously as the zone with Kjerulfia lundgreni and Holmia torelli. The former may belong to Wanneria, while the latter may be considered a subspecies of Schmidtiellus mickwitzi, the nominal subspecies of which is from the Estonian Lükati Sandstone. The Norretorp Formation also includes Holmia mobergi (a species that seems to be represented in the Lükati Sandstone) in unit la-alpha at Mjøsa in southern Norway, and in the Duolbasgaissa Formation in Finnmark, northern-most Norway. (See Bergström, 1980.) The correlation between unit la-alpha and the Duolbasgaissa Formation is somewhat strengthened by the occurrence in common of the characteristic trilobite trace Rusophycus dispar, which is known also from the Mickwitzia sandstone in Vestergötland, south-central Sweden. Additional fossils of correlational value occur in unit la-alpha at Mjøsa. One is the characteristic Spatangopsis, found elsewhere in the Mickwitzia sandstone and Lükati sandstone. Another is Platysolenites antiquissimus which has a long range extending downward from the



from the Mjåsa area. Both in Skåne and at Mjåsa the zone characterizes the lower part of a natural formational unit, deposited during a distinct transgression. This transgression brought the first non-olenellid trilobites, mainly species of Ellipsocephalus, Proampyx, Strenuaeva, and Comluelia. The recent discovery of what appears to be Calodiscus lobatus both in Skåne and in Jämtland (west-central Sweden) indicates a correlation with strata that contain the Dipharus attleborensis assemblage on both sides of the Atlantic (the top of the range of Callavia) and in Siberia. For instance, this assemblage is found at the upper end of the range of the olenellid Fallotaspis in Morocco, which is in accord with the find of a true fallotaspid, "Fallotaspis" ljungneri, obviously in the zone of the H. kjerulfi group at Laisvall in Lappland (Bergström, 1973). Olenellids characteristic of this zone are also found at Grlitz in Germany (GDR), where they are associated with protolenids (Lusatlops and Micmacca) and the eodiscid Serrodiscus speciosus silecius. The latter indicates a correlation with North American strata that have the Elliptocephala asaphoides

assemblage. In conclusion, the zone of the Holmia kjerulfi group appears to correlate with (part of) the Bonnia-Olenellus Zone in North America, with the top of the Callavia beds on both sides of the Atlantic, and with the top of the Atdabanian in Siberia.

#### Proampyx linnarssoni Zone

This zone characterizes the top of the natural formational unit referred to above in Skåne and Mjåsa. Evidence from Skåne (Bergström and Ahlberg 1981) indicates the possible presence of more than one trilobite zone, but the evidence is still too meagre. The solenopleurid genera are the same as in the underlying zone, but the species are mostly different, and there are no olenellids. The composition is very close to that of the so called Protolenus Zone in Poland, which is dominated by solenopleurid trilobites. This is the uppermost unit in the Scandinavian Lower Cambrian.

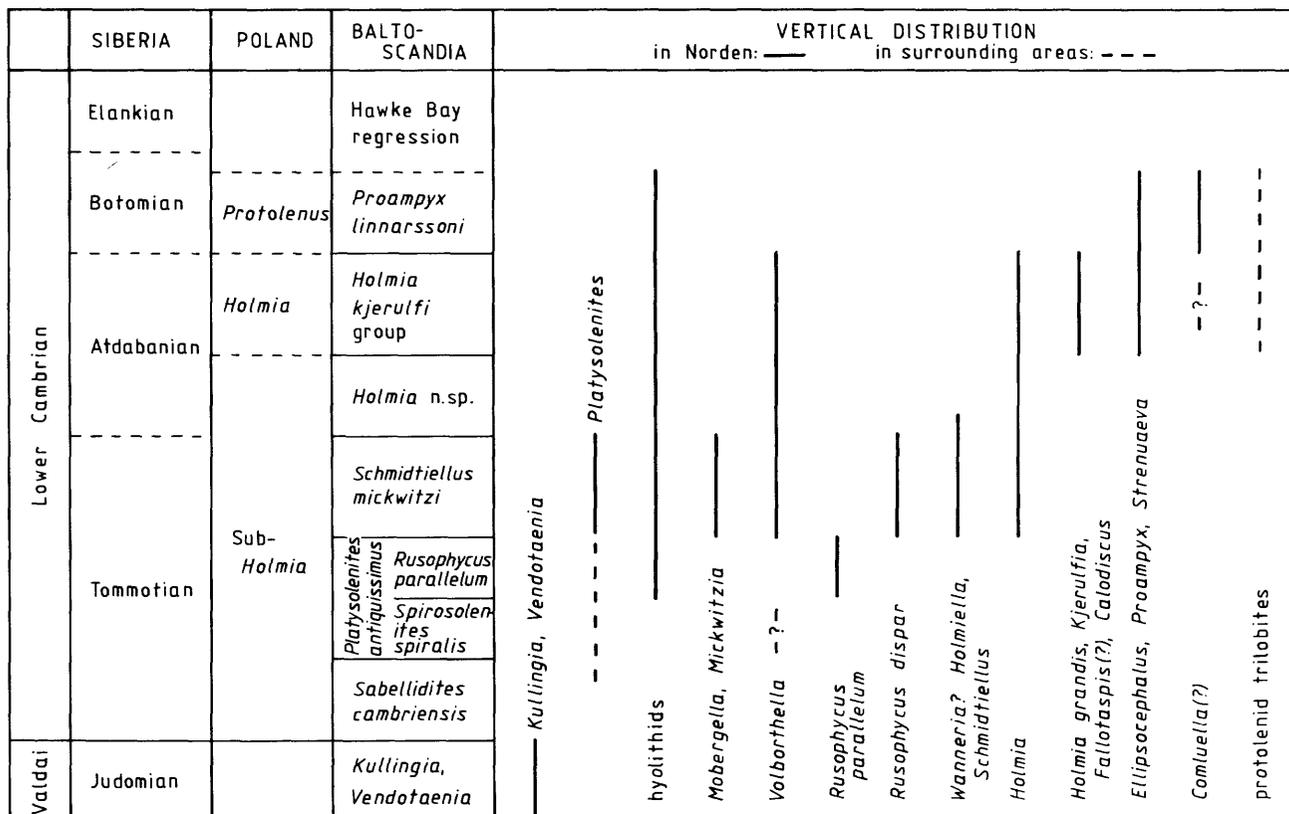


Figure 2.--Ranges of some important upper Vendian (Valdai) and Lower Cambrian fossils in Baltoscandia, Poland and Siberia. In addition to ranges shown, Schmidtellus is found in the Holmia "series" in Poland.

## Nontrilobite zones

Some nontrilobite zones have been recognized in the Lower Cambrian of Scandinavia. The "Hyolithus Zone" of the Caledonides is ill defined and needs no comment (See Fjøn, 1967). The Sabellidites cambriensis Zone is regarded as marking the base of the Cambrian but has not been identified in Scandinavia. The Platysolenites antiquissimus Zone is usually considered to extend from the base of the range of the zonal index to the base of the range of Volborthella, Mobergella, or the trilobites of the Schmidtellus mickwitzi Zone. Only the upper part of the P. antiquissimus Zone is identified with certainty in Scandinavia. This upper part is characterized by Holmia "stage" acritarchs (Vidal, this volume) and rare trilobite traces. The Volborthella and Platysolenites Zone corresponds to the interval where the two index forms overlap in range. As far as is known, the overlap seems to correspond more or less to the Schmidtellus mickwitzi Zone. If so, the Volborthella and Platysolenites Zone also corresponds roughly to the Mobergella holsti Zone, recognized in the west Baltic succession and in Poland, and as the Platysolenites and M. holsti Zone in southern Norway. The Volborthella tenuis Zone extends from the top of the Volborthella and Platysolenites Zone upwards without a distinct upper limit. Evidence from the Baltic indicates that Volborthella tenuis ranges at least into the Zone of the Holmia kjerulfi group. At Mjåsa, Volborthella tenuis is restricted to the Bråstad Shale and used therein, together with Holmia n. sp. ('Callavia'), as a zonal index.

**Acknowledgments:** A contribution to the PRECAMBRIAN-CAMBRIAN BOUNDARY PROJECT and PROJECT TORNQVIST (IGCP Accession in Numbers 29 and 86).

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## 8. VENDIAN AND CAMBRIAN PALEOGEOGRAPHY OF THE EAST EUROPEAN PLATFORM

By

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Combined Polish-Soviet research has produced a new stratigraphic scheme for the Vendian and Lower Cambrian of the East European platform (fig. 1), based on the vertical distribution of acritarch associations and other fossils. Detailed studies have been published in two series of monographs which were published in 1979. These data allow us to begin drawing lithologic-paleogeographic maps for small stratigraphic units.

Cambrian	Є <sub>2</sub>	Kibartu	<i>Ellipsocephalus politomus</i>
		Rausve	
	Є <sub>1</sub>	Vergale	<i>Strenuaeva primaeva</i> , <i>Holmia</i>
		Talsy	<i>Schmidtellus</i> , <i>Volbortella</i> <i>?Fallotaspis</i>
		Lontova	<i>Platysolenites</i> , <i>Aldanella</i> , <i>Anabarella</i> , <i>Sabellidites</i>
?	Rovno	<i>Platysolenites</i> (in upper part) <i>Sabellidites</i>	
Vendian		Kotlin	<i>Vendotenides</i>
		Redkino(Valday)	Soft-bodied fauna
		Drevljany = Volyń	

Figure 1.--Subdivisions of the Vendian and the Lower Cambrian of the East European platform.

Maps have been made for four Precambrian intervals (the Viljtchany, Volyn', Redkino, and Kotlin units) and four Cambrian intervals (the Rovno, Lontova, Talsy, and Vergale-Rausve units). The maps are for units small enough to allow us to reconstruct the development of the ancient Vendian-Cambrian basin on the East European platform and form a complete conception of the changes that took place at

the Precambrian-Cambrian boundary (fig. 2). Models of the separate subregions that served as initial data for the lithologic-paleogeographic schemes were prepared by B. Aren', V. Ya. Bessonova, A. P. Brangulis, V. A. Verikanov, V. I. Vlasov, V. V. Kirsanov, V. V. Kirjyanov, I. V. Klimovitch, K. Lenzion, K. A. Mens, L. T. Pashkyavitchene, E. A. Pirrus, L. V. Piskun, A. Yu. Rozanov, V. F. Sakalauskas, N. M. Tchumakov, and T. V. Yankauskas. The editors of the maps were V. Ya. Bessonova, A. P. Brangulis, V. A. Velikanov, V. I. Vlasov, V. V. Kirsanov, V. V. Kirjyanov, K. A. Mens, A. Yu. Rozanov, N. M. Tchumakov, and T. V. Yankauskas.

At the beginning of late Vendian Valday time (or Redkino time) a new structural plan of the East European platform appeared. This plan persisted in outline during the early Paleozoic. In Kotlin time (fig. 2A), we see some changes of this plan on the northwest, where the basin of sedimentation expanded to cover all of the territory of Estonia. However, there are no Kotlin deposits over the vast territories of Latvia, Lithuania, and the adjoining parts of Poland.

At the end of Kotlin time widespread regression took place, resulting in the erosion of uplifts and an increase in the deposition of red sandstones (the Reshma Formation) in some restricted basins. During the new transgression of the Rovno sea, quartz-glaucanite sandstones and very typical "blue clays" began to be deposited. The Rovno basin has approximately the same configuration as the Kotlin one, but it is narrower (fig. 2B). The axial part of the Rovno basin, where the Rovno horizon thickness is 50 m and even more, has probably migrated to the northwest.

The outlines of the Lantova basin (fig. 2C) are generally the same as those of the Rovno basin, but the Lontova basin was probably a bit broader. The types of rocks of the two basins are similar as well, though there are some layers of siltstone and fine-grained sandstones which constitute among the Lantova deposits. Everywhere in these rocks are grains of glauconite, which constitute the main difference between these deposits and the Kotlin ones in which glauconite is rare.

It is supposed that the Rovno and Lontova deposits formed in a shallow, well-aerated marine

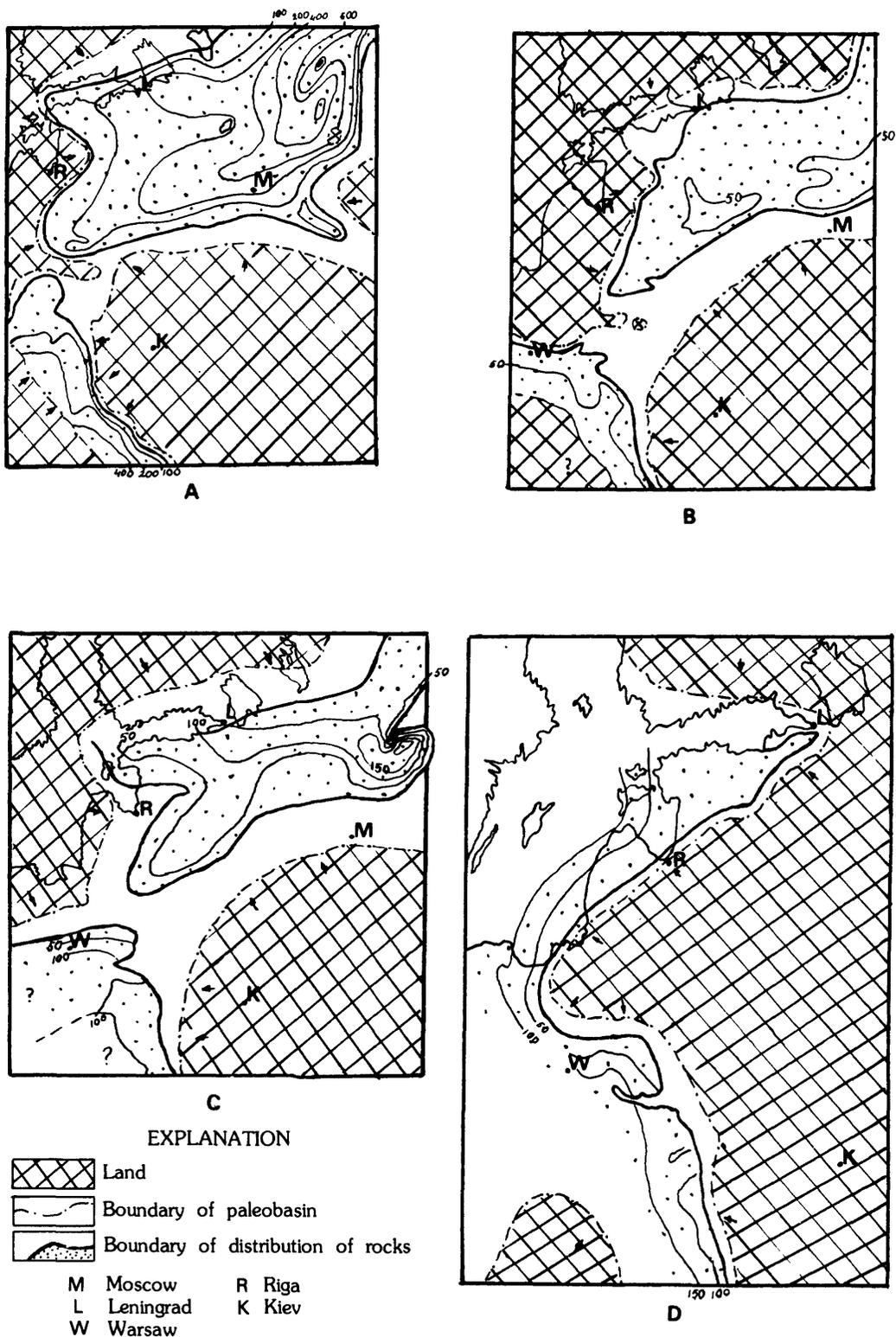


Figure 2.--Vendian and Lower Cambrian paleogeography of the East European platform. A, Kotlin time; B, Rovno time; C, Lontova time; D, Talsy time. Isopach contours in meters. For scale, distance from Kiev to Riga (K to R) is approximately 800 km.

basin favorable for the development of life. In Rovno time there were abundant Sabelliditida, whose first appearance is recorded in the Redkino deposits. The composition of the Rovno acritarch association is enriched by an increase in the diversification of species of Leiosphaeridia, by the appearance of Teophipolia laverata and Ceratophyton vernicosum, and by the appearance of Platysolenites in the uppermost part of the Rovno horizon. The organic world changed notably in Lontova time; in Lontova strata we observe diverse complicated trace fossils and numerous remains of Sabelliditida, Platysolenites, gastropods, hyolithids, and Hyolithelmintes. The acritarch associations, among which the most important are Granomarginata and Tasmanites, became greatly different.

In Talsy time (fig. 2D) the paleogeographic situation on the eastern European platform changed greatly. The Rovno and Lontova basins had inherited their general features from their Valday predecessor; the linear depressions situated between the Sarmatian and Baltic shields were extended during these two intervals. But beginning in Talsy time the general paleogeographic situation became basically different. In preceding ages the Moscow syncline was a permanent depression, but by Talsy time it no longer controlled a zone of sediment accumulation. The Baltic syncline now formed on the western part of the East European platform. We can observe only the eastern slope of this large structure, within which thickness of Talsy and younger units grows westward. The same situation, but with several alterations, is observed in Vergale-Rausve sediments, although they are characterized by facies that are a bit more diverse.

The Talsy horizon deposits are mainly represented by an alternation of clays and siltstones deposited in a shallow, warm basin favorable for the

existence of various organisms, among which we have found trilobites, brachiopods, hyolithids, and Hyolithelmintes, diverse deposit feeders and abundant acritarchs. Numerous species of the genus Baltisphaeridium appear in this horizon. As in the overlying Vergale-Rausve horizon, acritarchs form typical associations that allow us to make a detailed correlation of sections over vast areas.

While examining the history of the Vendian and Cambrian basins of the western part of the East European platform, we can record several changes, some of which coincide with those in the development of the organic world:

1. The beginning of formation of the Vendian Valday Series reflected a simultaneous change in structural plan. This moment coincides with the occurrence and settlement of the "White Sea biota," composed of multi-cellular organisms. This time is considered by some scientists to be the beginning of the Vendian.

2. The beginning of formation of the Rovno horizon represented some paleogeographic changes and a new transgression as well as a definite change in the dynamics and geochemistry of the basin. The turning point coincides with the appearance of the organisms traditionally assigned to the Cambrian (Sabelliditida) on the East European platform. However, at the boundary of the Rovno and Lontova horizons, where we detect true skeletal fossils of the lowermost Cambrian, we do not observe such noticeable paleogeographic changes.

3. The beginning of formation of the Talsy horizon was characterized by great changes in the paleogeography in the Baltic basin; it coincided with the appearance of trilobites, although the Baltic species are probably not as ancient as some other described trilobites.

## 9. FAUNAL SEQUENCE WITHIN THE LOWER CAMBRIAN "NON-TRILOBITE ZONE (S.L.) OF CENTRAL ENGLAND AND CORRELATED REGIONS

By

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In many sequences that span the uppermost Precambrian-Cambrian transition, small shelly fossils appear in facies that lack trilobites. Assemblages of such fossils have been used to delimit sub-trilobite units such as the Etcheminian of Newfoundland, the Tommotian of Siberia, the Subholmia beds of Poland, and the Non-Trilobite Zone of Britain (Matthew, 1899; Rozanov and others, 1969; Cowie and others, 1972). This biostratigraphic concept appears to have withstood the test of time, but its correlation is often dependent on stratigraphic position and the absence of trilobites, rather than on the presence of a distinctive assemblage. At Nuneaton in the English Midlands is a sequence of Non-Trilobite Zone (s.l.) fossils that allows correlation with other English rocks, as well as with faunas in North America, the Baltic, and Siberia. The aim of this paper is to document the vertical distribution of these fossils (following new discoveries and the study of established collections) and to consider, briefly, correlation of three main faunas that occur there.

The stratigraphy and lithofacies of the Hartshill Formation of Nuneaton has already been described (Brasier and others, 1978; Brasier and Hewitt, 1979). The Caldecote volcanics are equated with Charnia-bearing tuffs some 20 km to the northeast. They are intruded by markfieldites which, in Leicestershire, yield a Rb-Sr whole-rock age of 542±22 m.y. The Hartshill Formation overlies the Caldecote unconformably. At the base of the Hartshill is a sequence of as much as 250 m of coastal sandstones bearing the trace fossils Arenicolites, Didymaulichnus, Gordia, ?Psammichnites, Planolites and, just below the Home Farm Member, Isopodichnus. The latter member comprises about 2 m of conglomerates, sandstones, and condensed, red, nodular limestones with a relatively prolific fauna. The fragmentary fossils (mostly microfossils) first reported by Cobbold (1919) have now been studied in some detail at the type locality by microscopy of serial stained-acetate peels of vertical rock slices, of rock chips, and of residues obtained by standard conodont acid etching techniques, to yield data on preservation and abundance of taxa through the Home Farm into basal Purley Shale units. More than 10,000 shells and fragments were measured.

The vertical ranges of taxa in the Home Farm Member and higher beds are shown in figure 1. Sampling along the outcrop confirms a fairly uniform history along the 1 km of strike. The fauna of the Home Farm Member divides naturally into six successive assemblages:

- I. Total range of 'Obolella' groomi Matley; lower partial range of Sunnaginia imbricata Miss., of Hyolithellus micans (Billings), and of Micromitra phillipsi (Holl). Basal quartzose conglomerate (less than 0.5 m).  
'Obolella' groomi awaits proper taxonomic revision; this is its first record from Nuneaton. The identity of Sunnaginia with S. imbricata is not accepted by Matthews and Cowie (1979). H. micans in this bed is distinctively large (less than 1.7 mm diameter) and has prominent internal rings, external transverse grooves, and external growth lamellae. M. phillipsi specimens are also large (less than 14 mm).

This wholly phosphatic assemblage is allochthonous: the specimens are size sorted, fragmentary, and disarticulated within a current-bedded conglomerate. Less robust shells may have been destroyed in transport or diagenesis.

- II. Lower partial range of Coleoloides typicalis Walcott, concurrent with H. micans and M. phillipsi. Calcareous cemented sandstone above quartzose conglomerate (less than 0.6 m).

The scarce specimens show signs of transport. C. typicalis occurs as phosphatised fragments.

- III. Total range of Camenella baltica (Bengtson), C. cf. kozlowskii (Miss.), Eccentrotheca kanesia Landing and others, protoconodont aff. Amphigeisina danica (Poulsen); upper partial range of S. imbricata; lower partial range of Torellella lentiformis (Sysoiev), 'Hyolithes' alatus Cobbold, and Helcionella paupera (Billings). Bed 1 of the Hyolithes Limestone (especially the phosphatised limestone conglomerate; less than 0.2 m).

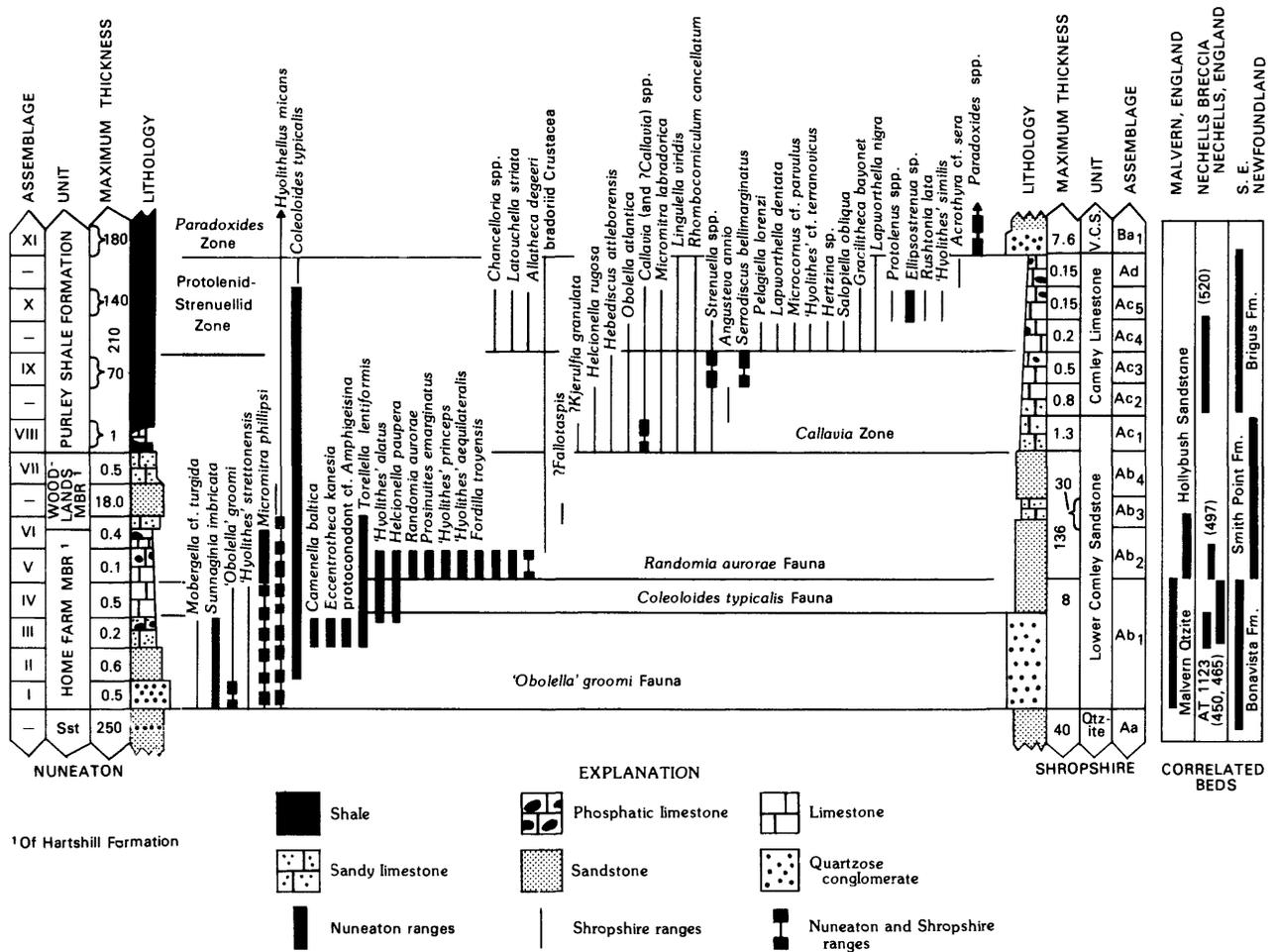


Figure 1.--Composite vertical ranges of selected taxa through the Lower Cambrian of Nuneaton and Shropshire, England. Correlated beds are shown on the right. *Callavia* and higher zonal ranges based on sources in Rushton (1974).

*Camenella* here includes *Tommotia baltica* and *C. garbowskae* listed by Brasier and others (1978). The protoconodont (*Hertzina* sp. of Matthews and Missarzhevsky, 1975) has a distinctive triangular cross section. *T. lentiformis* here includes forms previously referred to *T. cf. T. biconvexa* Miss. as well as some resembling *T. curvae* Miss. '*Hyolithes*' *alatus* may belong to *Burithes* Miss. *Helcionella paupera* includes *H. abrupta* Shaler and Foerste, interpreted as the juvenile form. *Coleoloides typicalis* includes *C. trigeminatus* Miss., *C. bornholmensis* Poulsen, *C. paucistriatus* Poulsen and *C. multistriatus* Cobbold as growth stages; *Glauderia mirabilis* Poulsen is regarded as a variant of this species.

This assemblage is mostly phosphatised, fragmented and worn, and shows lithological evidence of hardground development and reworking. *H. micans* is abundant and of greater diameter here than in higher calcareous beds; it exceeds *T. lentiformis* in measured volumes of shell fragments and shell cavity per kilogram of rock. Slow deposition and non-sequences are inferred.

- IV. Lower partial range of hexactinellid sponge spicules (cf. *Protospongia*); abundant *C. typicalis* and *T. lentiformis*; *Helcionella paupera* present but sparse. Beds 2-10ii of the *Hyolithes* Limestone (less than 0.5 m).

The calcite hexactinellid spicules may have originally been of opaline silica.

Coleoloides typicalis predominates, as colonies in life position at several levels but mostly disorientated or nested together by currents or bioturbation. T. lentiformis exceeds H. micans in the measured volume of shell fragments of and shell cavity per kilogram of rock from beds 2-11 inclusively. Deposition was slow, perhaps with alternating periods of soft-bottom colonisation (by Coleoloides), and lithification that favoured a hardground fauna (perhaps including sponges, Torellella, and Helcionella).

- V. Total range of Randomia aurorae Matthew, Latouchella striata Cobbold, Prosinuites emarginatus (Cobbold), Fordilla troyensis Barrande, Allatheca degeeri (Holm). 'Hyalithes' princeps Billings, 'H.' aequilateralis Cobbold; acme of Helcionella paupera, 'Hyalithes' biconvexus Cobbold; upper partial range of the latter two and of sponge spicules. Bed 10iii of the Hyalithes Limestone (less than 0.1 m).

Randomia aurorae is here reported from England for the first time, though Cobbold had collected some specimens; fragments described as ?Callavia (for example, Cobbold and Pocock 1934, pl. 39) are of Randomia. 'H.' princeps is a senior synonym of H. excellens Billings and H. willsi Cobbold. Only one valve of Fordilla is known.

This diverse assemblage is found in a thin coquina with abundant Hyalitha (especially A. degeeri) and is associated with phosphate and Fe-Mn stromatolite intraclasts. Both current orientation and nesting of shells indicate transportation of fossils, but fragmentation and wear were not great. Slow deposition with some current winnowing would account for the coquina, the authigenic glauconite-coated shells, and the large glauconite grains.

- VI. Acme of Hyalithellus micans; partial range of C. typicalis, T. lentiformis, M. phillipsi. Beds 11-12 of Hyalithes Limestone (Home Farm Member); Bed 13 (basal Woodlands Member); together less than 0.4 m).

Beds 11 and 12 are recrystallised sparry limestones with vugs, sheet cracks, neptunian dykes, and in situ and transported Fe-Mn stromatolites. Fe-Mn replacement and glauconite void filling of shells is common in beds 12 and 13; the latter is a current-bedded sandstone with calcareous cement in which fossils occur as sparse, size-sorted fragments. Hyalithellus micans

exceeds both C. typicalis and T. lentiformis in measured volumes of shell fragments and of cavity per kilogram of rock, though H. micans specimens are small (less than 0.7 mm diameter). Coleoloides specimens are also small (less than 0.9 mm diameter) in beds 11-13. Very slow deposition and restricted ecological conditions are inferred for beds 11-12. Reworking and rapid deposition by tides and storm are inferred for bed 13. The dominance of phosphatic forms may, in part, be due to selective preservation, as in the basal beds.

About 18 m of sheet sandstones (Woodlands Member) intervene between bed 12 and some thin calcareous lenses at the top of the members; these contain C. typicalis and Torellella sp. (assemblage VII). Nodules about 1.5 m above the base of the overlying Purley Shale Formation contain C. typicalis, hexactinellids, and ?Callavia fragments (assemblage VIII). The higher assemblages with trilobites, here called IX-XI, are reviewed by Rushton (1974).

## CORRELATION

Whereas Nuneaton has a very condensed Non-Trilobite (s.l.) sequence (approximately 20 m) overlain by more than 140 m of Callavia Zone and Protolenid-Strenuellid Zone shales, the reverse is seen in Shropshire. At Comley and at The Wrekin, these trilobite zones are condensed to approximately 2 m of calcareous sandstone and limestone, overlying as much as 190 m of older clastics. These rest unconformably on a granophyre intrusion with a Rb-Sr whole-rock age of  $533 \pm 13$  m.y. (Patchett and others, 1980). The basal Wrekin Quartzite (approximately 40 m) contains a few probable Diplocraterion traces, and so a Precambrian age is precluded. The overlying Lower Comley Sandstone (approximately 150 m) contains a non-trilobite fauna (for example, Rushton, 1974), which allows a preliminary correlation of the Lower Cambrian of Nuneaton and Shropshire (fig. 1). The composite range chart for England is made possible by correlation of the first occurrences of 'O.' groomi, M. phillipsi, H. micans (and variants), A. degeeri, Callavia (including ?Callavia), Serrodiscus bellimarginatus (Shaler and Foerste), and Paradoxides spp. (plus other P. oelandicus Zone trilobites). Fossils from the Malvern Quartzite (for example, Rushton, 1974) and clasts in the Permian Nechells Breccia (for example, Boulton, 1924) have also been examined by us. The three successive faunas that may be distinguished in the non-trilobite zone (s.l.) are outlined below.

## THE 'OBELELLA' GROOMI FAUNA

An assemblage of 'O. groomi, and H. phillipsi provides the lowermost shelly fauna at Nuneaton (Assemblage I), Shropshire (Ab<sub>1</sub>), and Malvern (Malvern Quartzite). The associated fauna of either Camenella baltica (from Nuneaton III, and the Nechells Breccia and recently from the Malvern Quartzite) or Mobergella cf. turgida (Ab<sub>1</sub>) allows direct comparison with the Mobergella fauna of the Baltic area (Bengtson, 1977).

Mobergella is typical of the uppermost Tommotian Stage in Siberia thus the Baltic Mobergella and C. baltica are thought to be of this age (Bengtson, 1977). But at Nuneaton, Mobergella is replaced by Sunnaginia imbricata, formerly regarded as a lower Tommotian microfossil (Roazanov and others, 1969), hence the suggestion that condensed or reworked lower Tommotian material is present in the lower Home Farm Member (Brasier and others, 1978). However, this interpretation must be questioned by the recent discovery of S. imbricata with Eccentrotheca kanesis from the Callavia Zone of Nova Scotia (Landing and others, 1980). The lipped hyoliths associated with this fauna in England ('H. strettonensis and 'H. alatus) would not support a lower Tommotian correlation.

The 'O. groomi-Mobergella fauna is often found in conglomeratic or sandy facies. It may therefore be transported and reworked; it is also likely to be a diachronous facies fauna (as shown for example, by the occurrence of some elements with Callavia Zone trilobites in Nova Scotia, though condensation and reworking cannot be discounted here).

## THE COLEOLOIDES TYPICALIS FAUNA

Assemblage IV at Nuneaton, with dominant C. typicalis and rare hyoliths, is a partial range assemblage with no diagnostic elements. A similar fauna is not seen in Shropshire but occurs in Newfoundland with a comparable stratigraphic position; that is, above a middle or upper Tommotian Aldanella fauna and below a Randomia fauna (S. Bengtson, personal commun., 1980). But the value of the C. typicalis fauna for correlation is limited since this species, H. micans, and Hexactinellida are part of a facies fauna that recurs without identifiable trilobites or hyoliths in the Protolenid-Strenuellid Zone of Shropshire (bed Ad).

## THE RANDOMIA AURORAE FAUNA

Assemblage V with R. aurorae and abundant A. degeeri at Nuneaton is tentatively correlated with an A. degeeri, H. princeps assemblage at Nechells, with a sparse A. degeeri(?) assemblage at Comley (Ab<sub>2</sub>), and

on position alone with the Acrothele prima assemblage at Rushton, near The Wrekin. A. degeeri ranges from upper Tommotian to Atdabanian in Siberia, with an acme in the latter unit (Roazanov and others, 1969). 'Orthotheca' pugio Matthew (cf. A. degeeri) occurs in the Smith Point Formation of Newfoundland with Randomia aurorae, Fordilla troyensis, Helcionella paupera, 'Hyolithes' princeps, 'Orthotheca' sica Matthew (cf. 'H. aequilateralis), Coleoloides typicalis, Hyolithellus micans, and others (Matthew, 1899; Walcott, 1900). Matthew considered R. aurorae characteristic of his Etcheminian fauna, but Randomia is missing from otherwise similar assemblages in Massachusetts (see Grabau, 1900); this taxon compares closely with Tannuella elata Miss. from the Atdabanian of Siberia.

Elements of the Randomia fauna also occur in Scandinavia, especially in the Green Shales of Bornholm, which contain Prosinuites emarginatus, Fordilla troyensis, C. typicalis and variants, and H. micans (Poulsen, 1967); the presence of Volborthella and ?trilobites in these shales and in the similar Norretorp Sandstone of southern Sweden makes likely a correlation with the Tommotian-Atdabanian boundary beds (Poulsen, 1978; Ahlberg and Bergström, 1978).

Elements of the Randomia fauna of Nuneaton are therefore found just below the Callavia Zone of North America and in the Schmidtellus mickwitzii-Holmia mobergi Zone of Scandinavia. Their position below Callavia Zone beds makes likely a partial correlation with the Fallotaspis Zone of Fritz (1972). A carapace of ?Fallotaspis from bed Ab<sub>3</sub> at Comley (Hupe, 1952) also suggests this possibility.

It should be stressed that elements of the Randomia fauna occur in the Callavia and Protolenid-Strenuellid Zones of England and elsewhere, but Randomia aurorae, 'Hyolithes' princeps and Prosinuites emarginatus appear to provide time-restricted markers of international value. Analysis and systematic revision of hyolith faunas is needed, however, if an improved correlation of the Tommotian-Atdabanian and the Non-Trilobite Zone is to be achieved.

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## 10. THE BURGESS SHALE PROJECT<sup>1</sup>

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Walcott's (1911a,b,c, 1912, 1919, 1920, 1931) papers on the Burgess Shale fossils were preliminary in nature, largely because many were written before the bulk of his collections were made. Subsequent publications on the fauna relied heavily on Walcott's original descriptions. Only Simonetta (1962, 1963, 1964, 1970; Simonetta and Delle Cave, 1975, 1978; Delle Cave and Simonetta, 1975) made any large-scale examination of additional material, but he neither prepared the fossils nor satisfactorily illustrated the evidence upon which many of his interpretations were based. The first Geological Survey of Canada (GSC) collecting expedition, which launched the reinvestigation of the Burgess Shale, took place in 1966 (Whittington, 1971a), fifteen years ago this summer.

The GSC expeditions recorded in detail for the first time the levels in the quarry from which specimens were collected. A knowledge of which species occur together at particular horizons may be useful for assessing interactions between them, but it appears that a similar community was being sampled throughout the Walcott quarry, a community made up of infaunal, epifaunal and some pelagic components (Conway Morris, 1979b). Walcott's collections amount to more than 60,000 specimens. Although the GSC collected about 20 percent of that figure in two seasons, no new species has yet been positively identified in their material. These collections have proved invaluable, however, together with specimens collected from the talus by a Royal Ontario Museum party in 1975 (Collins, 1978), in supplementing the evidence for the morphology of some species.

The Burgess Shale project is a classic example of what can be achieved by the painstaking application of traditional techniques. Walcott, or his preparators, occasionally used a fine chisel and hammer to remove matrix covering parts of the fossils, but the specimens had not been extensively prepared prior to the reinvestigation. We employ a sharpened needle

mounted in a percussion hammer and another one driven by a dental drill not only for flaking off matrix but, more importantly, for carrying out "paleodissections"--removing successive layers of a fossil to reveal those beneath. This approach has yielded a wealth of new information, particularly on the arthropods, which are preserved in layers (exoskeleton, body, and overlapping appendages) separated by a thin veneer of matrix. The fossils are not suitable for study by x-radiography, and the kind of detailed microstructure that is investigated by scanning electron microscopy is not preserved.

Most of Walcott's photographs of the Burgess Shale fossils took advantage of their reflectivity to provide a contrast against the dark matrix. Many of the prints were retouched to enhance details that were not readily visible. Whittington discovered that the use of ultraviolet illumination usually gives the best photographic results, particularly in the case of unweathered specimens. If the light is directed at a low angle the fossil appears dark against a lighter matrix; different types of features become more evident when different directions of radiation are used. Features of some specimens are more readily photographed in reflected ultraviolet light, and contrast may sometimes be increased by covering the specimens with a film of water overlain by a thin glass plate. Oxidized specimens are ochreous in color and contrast with the matrix. This contrast may be emphasized by submerging the specimen in alcohol and photographing it in ordinary tungsten light. In some cases it is necessary to publish several photographs taken under different conditions to illustrate the evidence for a particular interpretation.

Considerable use is made of camera lucida drawings in the course of the research, to record details prior to preparation and to combine the evidence of both part and counterpart of a specimen, for example. Many of these drawings have been published alongside the plates to clarify the evidence for the interpretation of the morphology of particular specimens.

Since 1966 more than 30 papers have been published on the Burgess Shale fauna and more are in progress. The relative abundance of the different taxa has been documented by Conway Morris (1979b, and

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<sup>1</sup>The display to which this paper relates was prepared by the author and F. J. Collier (National Museum of Natural History, Washington, D. C.) with assistance from S. Conway Morris, J. K. Rigby, James Sprinkle and H. B. Whittington.

this volume). Of the 44 genera of arthropods (nearly 40 percent of the total), only 14 are trilobites. The appendages of only two of these are well known. Whittington's (1975b, 1980a) reinvestigation of Olenoides serratus revealed only three pairs of biramous appendages in the cephalon (as opposed to the four described by previous authors) in addition to the antennae, an arrangement similar to that observed in later, well preserved trilobites such as Triarthrus and Phacops. He also showed that the limbs interact in the midline the whole length of the trunk and that the spines on the coxae and inner rami suggest a predatory as opposed to filter feeding habit. Whittington (1977) demonstrated that Naraoia is also a trilobite. It was assigned by Walcott (1912) to the branchiopod Crustacea and was considered by various later authors to be a trilobite, a xiphosuran or a "trilobitoid". Some of this confusion arose from the misinterpretation of the lectotype, in which overlapping appendages extending beyond the posterior shield are suggestive of an abdomen or telson. Naraoia, like Olenoides, has 3 pairs of biramous appendages in addition to the antennae in the cephalon, and massive spiny gnathobases, presumably for predation.

Walcott classified the 30 genera (25 percent of the total) of "non-trilobite" arthropods as either Branchiopoda, Malacostraca, Trilobita, or Merostomata (all of which were then considered Crustacea). Briggs (1977, 1978) has shown that the bivalved Canadaspis perfecta is a phyllocarid crustacean. It displays the characteristic division of the trunk into thorax and abdomen but is primitive in the similarity between the posterior cephalic appendages and those of the trunk (in which respect it resembles Hutchinsoniella). Some other bivalved genera show a more equivocal affinity with the Crustacea (Briggs 1976, 1981), but the majority of the Burgess Shale arthropods clearly do not belong to any Holocene taxon.

Aysheaia, for example, was assigned by Walcott (1911c) to a new family of polychaetes, but its similarity to the onychophorans was soon recognized and it has been classified with them by most subsequent authors. Whittington (1978) revealed the detailed morphology of the head region for the first time and suggested that Aysheaia may have preyed on sponges. The terminal mouth and single pair of modified cephalic limbs (for grasping sponges?) are primitive features. Aysheaia is not an onychophoran, but may represent the type of morphology from which the ancestral uniramians were derived. Marrella splendens was classified by Walcott (1912) in a new family of trilobites, and was subsequently regarded, like many other Burgess Shale arthropods of uncertain affinity, as a trilobitoid (Whittington 1971b). The reinvestigation has shown that the "trilobite limb" is not a well defined structure that can be used as a

reliable indication of affinity. The complex problem of determining interrelationships between the Burgess Shale arthropods is presently under review as the descriptive work nears completion (Briggs and Whittington, this volume). Some genera originally interpreted as arthropods have undergone more radical reinterpretation. The strange animal Opabinia, nor example, was assigned by Walcott (1912) to the branchiopod Crustacea, an interpretation accepted by most subsequent authors, although Starmer (1944) classified it as a trilobitomorph. Whittington (1975a) maintains that Opabinia is neither arthropod or annelid, but represents a different early group of segmented animals (a new phylum).

The 18 genera of sponges (15.5 percent of the total), of which 13 were erected by Walcott (1920) for Burgess Shale species, make up the best represented phylum after the arthropods. They include demosponges, hexactinellids, and heteractinids (calcareous sponges) and are presently under study by J. K. Rigby. The fauna includes more than 50 percent of the known genera from the North American Cambrian, a number of which are unknown outside the Burgess Shale (Rigby, 1976).

The lophophorates (eight genera, 6.5 percent of the total) are mainly brachiopods and are exceptional only in the preservation of the pedicle and mantle setae in two species (Conway Morris, 1976). S. Conway Morris (1976) has interpreted a unique, previously undescribed specimen as a conodontophorid, Odontogriphus omalus; it has the simple conodonts forming a horse shoe-shaped line of supports for the tentacles of a lophophore around the mouth. The body is flattened and segmented, and the animal was apparently pelagic.

The priapulids are a phylum of infaunal marine worms with an annulate trunk and a spiny, retractable proboscis used in burrowing and feeding. Walcott (1911c) assigned Ottoia, the most abundant of the seven Burgess Shale genera (6 percent of the total) to the Gephyrea, a group comprising the priapulids, sipunculids, and echiuroids, now considered polyphyletic. Conway Morris (1977b) has shown that Walcott mistook other priapulids for polychaetes and in one case for an arthropod carapace. The Burgess Shale priapulids fall into at least 5 families and are much more diverse morphologically than the few living genera.

Walcott (1911c) assigned most of the worms that he described to the polychaetes. Conway Morris's (1979a) restudy of the class revealed only six genera (5 percent of the total) three of which are based on species originally described by Walcott and referred to Canadia. They show a diversity similar to that of the priapulids (at least five families) but are much less abundant. The polychaetes may have included nektobenthic as well as infaunal forms.

The fauna includes five genera (4 percent of the

total) of hemichordates and chordates. The most interesting of these, Pikaia gracilens, was described by Walcott (1911c) as a polychaete. The trunk displays a longitudinal bar and sigmoidally deflected myotomes, however, which have been interpreted by Conway Morris (1979b) as a notochord and myotomes respectively, suggesting that Pikaia is one of the earliest chordates.

There are five genera of echinoderms (4 percent of the total). The most abundant is Eldonia ludwigi, described in one of Walcott's (1911b) earliest papers on the fauna and interpreted as a pelagic holothurian, a classification recently upheld by Durham (1974). Walcott collected some specimens of the much rarer Echmatocrinus, the earliest known crinoid, but did not describe or name them. Sprinkle (1973) has shown that this genus is irregularly plated and was attached by a plated holdfast rather than a stem. An edrioasteroid and two eocrinoids were apparently unknown to Walcott.

Only two of the four genera (3.5 percent of the total) of coelenterates were known to Walcott and the group has yet to be restudied. He described Mackenzia costalis as a holothurian (Walcott, 1911b) but it is now considered an actinarian (Conway Morris, 1979b). The medusiform morphology of Peytoia nathorsti led Walcott (1911b) to refer it to the Scyphomedusae but it is unlike living forms and its affinities are uncertain (Conway Morris, 1978).

Two mollusks, Scenella and Hyolithes, are abundant in the Burgess Shale (Yochelson, 1961). They both have mineralized shells and were already known from elsewhere. They were classified by Walcott as gastropods, but Scenella is now considered a monoplacophoran, and Hyolithes is a separate class of the Mollusca (or a new phylum; Runnegar, 1980). Walcott's (1911c) figures present specimens of Hyolithes with the appendages (helens) attached. The rarer Wiwaxia corrugata was assigned by Walcott (1911c) to the polychaetes; it remains to be restudied, but the observation of a radula by Conway Morris (1979b) suggests that it may be related to the mollusks.

Walcott followed contemporary classifications of the invertebrates and placed the Burgess Shale animals in existing phyla and classes and for the most part, existing orders. The reinvestigation has shown that some 19 genera (16 percent of the total), including Opabinia mentioned above, do not fall readily into even living phyla, and represent distinct and hitherto unknown body plans (Conway Morris, 1979b, Conway Morris and Whittington, 1979, Whittington, 1980b). The aptly named Hallucigenia, rescued by Conway Morris (1977) from obscurity in the polychaete genus Canadia, to which it was assigned by Walcott (1911c), is one of the most abundant and bizarre of these. The majority await thorough investigation.

The most obvious result of the reinvestigation of

the Burgess Shale is the publication of well documented data on the morphology and diversity of the fauna. This information is providing a basis for additional general conclusions regarding the early radiation of the metazoa and, through comparisons with later faunas, their subsequent evolution.

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## 11. RELATIONSHIPS OF ARTHROPODS FROM THE BURGESS SHALE AND OTHER CAMBRIAN SEQUENCES

By

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Appendage-bearing arthropod specimens representing 19 genera, found in old and new collections from the famous Middle Cambrian Burgess Shale, have been described in detailed studies now published or in press. Nine of these genera were grouped with others in various orders and subclasses within the Class Trilobitoidea, and this class was grouped with Trilobita into the subphylum Trilobitomorpha by Størmer (1959), in on the assumption that all had trilobite-like appendages. This assumption has not been substantiated; the species show such a wide diversity of morphology that a partial appreciation of it led Simonetta to propose eight new orders to accommodate particular species. (See Simonetta citations in Briggs, this volume.) Discussion of these and other named taxa is beyond the scope of the present paper. Of the genera considered here, two (Canadaspis and Perspiscaris) have been referred to Crustacea (Waptia probably also belongs here), Olenoides and Naraoia are trilobites, while the uniramous Aysheaia stands apart from all others, as it lacked a sclerotized exoskeleton. In the remaining genera thus far studied (this excludes Emeraldella and Helmetia), each type species has unique characteristics, while those shared tend to be generalized and common to many arthropods. Relationships between these contemporaneous species are, therefore, far from obvious, and possible ancestral forms are unknown. We have used two methods in a preliminary attempt to reveal relationships between these Burgess Shale genera and the only other two Cambrian forms in which appendages are known. These are the Upper Cambrian Phosphatocopina from Sweden (the genera Vestrogothia and Falites being considered as a single unit), and Aglaspis from the Upper Cambrian of Wisconsin, though the appendages of the latter are incompletely known.

In the first method a series of 65 morphological characters were selected, each of which was scored according to its absence, presence, or state of development. For example, the body may or may not show trilobation, whereas the carapace, if present, may have been bivalved, with or without a rostrum, etc. Each genus is thus an entity characterized by a unique list of attribute states. The principal-components analysis we used considered the entities as points in multidimensional attribute space and

produced a three-dimensional system of coordinates by plotting the position of the genera relative to the three largest mutually perpendicular axes (eigenvectors). The eigenvalues corresponding to the first three eigenvectors show that they account for 35.6 percent of the ordination. All the attributes were given equal weight. The genera are linked by the minimal spanning tree (the shortest connected graph without closed loops joining all the points in attribute space) which links nearest neighbours. We gratefully acknowledge the advice and assistance of Dr. J. T. Temple, Birkbeck College, in running the programmes on the University of London computer. The resulting plot (fig. 1) is an assessment of similarities, which may reflect parallelism or convergence rather than relationship. Some shared characters, such as the large number of trunk segments in Branchiocaris and Odaraia, are not reliable indicators of affinity, and the significance of special characters shared by particular entities may not be evident.

Figure 1 reveals a wide spread with only one obvious cluster. Seven genera have Alalcomenaeus as their nearest neighbour, radiating out from it in morphological space. Closest is Actaeus, which differs in the appendages of cephalon and trunk and in the number of trunk somites. Actaeus is greatly similar to Leancoilia, the differences between them seemingly of minor importance. The wide separation between the two genera on the Y3 axis is a distortion introduced by the lack of information on the inner ramus of trunk appendages. Leancoilia and Naraoia also plot close to Alalcomenaeus. None of the characters shared by these genera, however, are unique or even rare in the sample, and there is no evidence to suggest an affinity between Naraoia and the other two. Leancoilia and Alalcomenaeus differ in the number of trunk somites, in the nature of the telson, and in important details of the appendages, but may nevertheless form a group with Actaeus. Further from Alalcomenaeus are Sidneyia, Habelia, Molaria, and the new genus. Many of the characters shared by these arthropods are either of minor importance or common to almost all the sample. They are united, however, in having a cephalic shield, which is associated with a series of dorsal tergites on the trunk. Outside the group this exact feature is found only in Aglaspis and Olenoides, and a modified form is

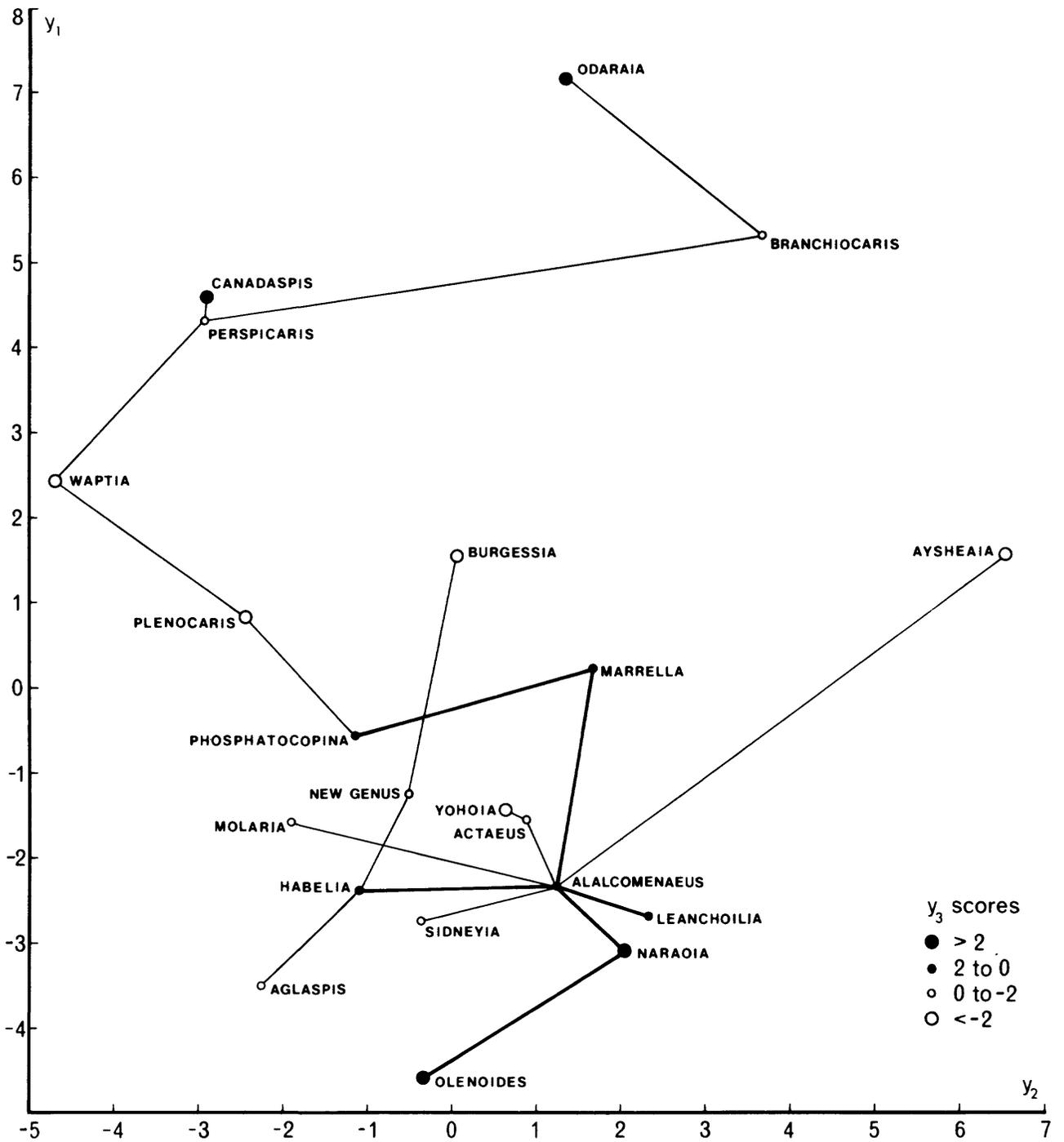


Figure 1.--Principal-components analysis ordination of 21 Cambrian arthropod genera, based on 65 attributes, with superimposed minimal spanning tree (MST). Plotting is on the first and second eigenvectors ( $y_1$  and  $y_2$ ) of the correlation matrix, with scores on the third eigenvector indicated by symbols. Links of the MST are thickened where they join with entities having positive scores on the third eigenvector.

found in Yohoia. These latter three arthropods lie on the fringes of the cluster, as does Marrella. The exoskeletons of Aglaspis and its nearest neighbor Habelia are broadly similar, although the number of trunk somites differs, and they alone share a spinelike telson. They differ, however, in important characters, including the number of cephalic appendages and the presence of a postventral plate in Aglaspis, as well as in the details of the appendages and telson. Yohoia and Actaeus share no characters that are unique, but share some common to few other genera: that is, they lack of an annulated antenna, certain of their cephalic appendages are specialised distally for feeding, and they have a flattened, paddlelike telson. However, the special characters of each are so different that they do not suggest relationship.

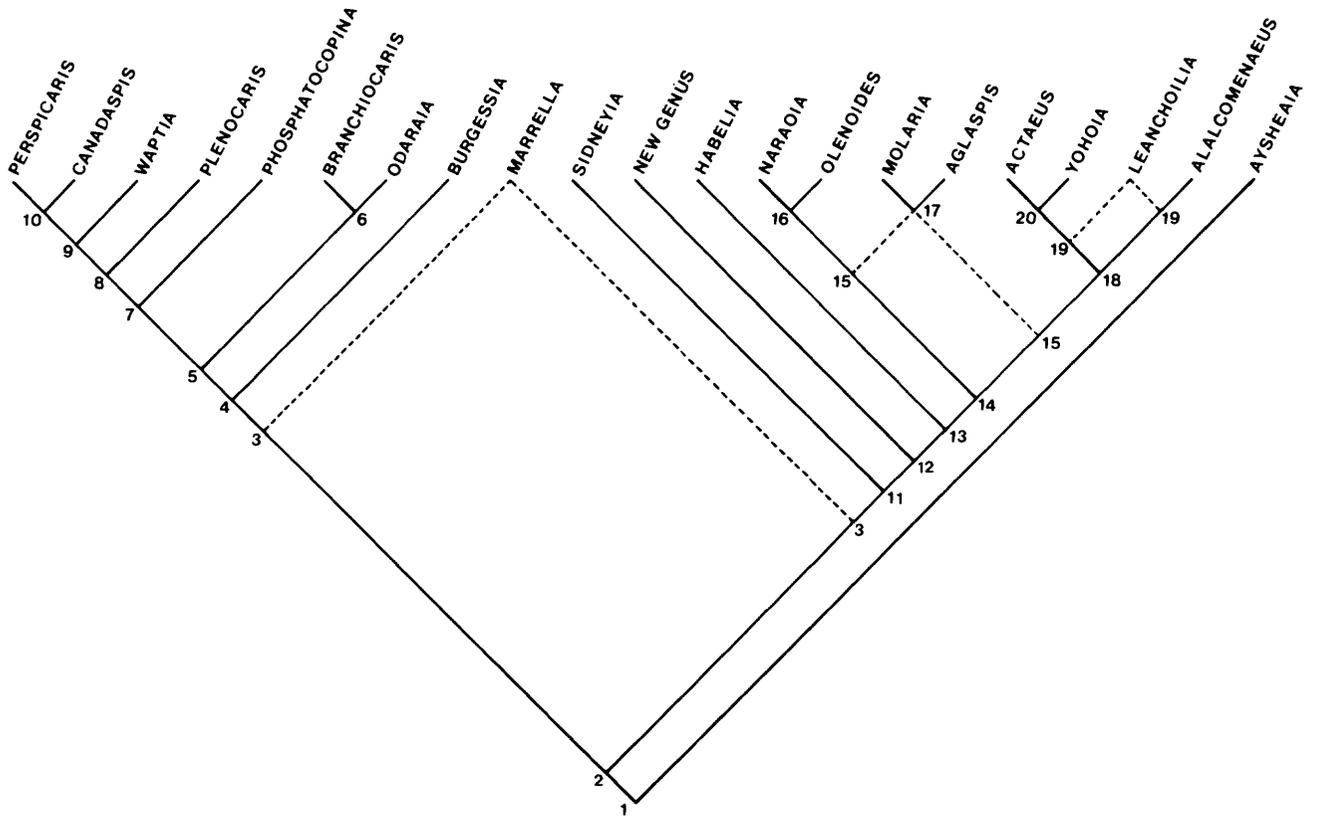
A second loose cluster is formed by Waptia and Perspiscaris together with Plenocaris and Canadaspis, which are slightly distant. Waptia and Perspiscaris differ mainly in the number of posterior cephalic appendages and the number of trunk somites. Both have pairs of antennae, one reduced, as in Canadaspis, and this latter genus has 15 trunk somites, as does Perspiscaris. The separation on the Y3 axis of Perspiscaris and Canadaspis is because of differences in the telson: the former has a caudal furca, Canadaspis lacks one. The similarity of the other two genera to them suggests the possibility of affinity within the group.

The genera considered here are separated by wide morphological gaps. This diversity is evident even in those that are obviously related: the trilobites Olenoides and Naraoia are placed in separate orders, the Crustacea Perspiscaris and Canadaspis in distinct families. In our second method we attempted to assess the relative significance of the various similarities between genera by drawing cladograms. Because of the many uncertainties it has proved impossible to draw a cladogram that we consider an acceptable representation of possible relationships between the arthropods. Apart from the difficulty of recognizing the results of convergent or parallel evolution, it appears that the evolution of different characters occurred at different rates in different lineages (mosaic evolution), exacerbating the problem of deciding which characters are significant at which level in the nested hierarchy. Canadaspis and Perspiscaris, for example, show no clear separation of posterior cephalic appendages from those of the trunk, and yet the latter is clearly divided into two tagmata. Actaeus and Alalcomenaeus have only one

tagma in the trunk, and yet four pairs of appendages (none a uniramous annulated antenna) clearly belong to the head. In addition, we cannot be sure that we are comparing homologous characters. Thus the segments in the cephalic region, their appendages, and the position of the mouth, so important in the taxonomy of Holocene arthropods, cannot be used with the same confidence in the fossils. Further, a number of obviously derived characters occur in only one genus, and are therefore of no use in determining relationships.

Some of these difficulties are illustrated by the cladogram (fig. 2). The first dichotomy is drawn at arthropodization, the development from a soft-bodied animal with paired limbs of a similar animal with a sclerotized, jointed exoskeleton, which separates Aysheaia from the rest. The second major division separates genera that have a carapace extending posteriorly beyond the cephalon from those that have a cephalic shield with tergites. Both of these developments may have occurred more than once, contrary to the implication of the cladogram. In the group characterized by a cephalic shield and trunk tergites, the incorporation of successive appendages into the head is used to provide a nest of sets. This division is based on assumed homologies which may not be valid. The grouping of Branchiocaris and Odaria depends on their possession of telson processes, but such a similarity may result from convergence. The other characters shared by these genera are symplesiomorphic. The large morphological gaps between the species result from unknown evolutionary patterns, which extend back into the Precambrian; similar results of such patterns are manifest in other groups, such as the echinoderms. The independent lines of evolution displayed by these arthropods pose problems of classification which we are continuing to explore.

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**Figure 2.** One hypothesis of interrelationships of Cambrian arthropod genera. Key to synapomorphies as follows:

1. Serial segmentation, paired appendages
2. Jointed exoskeleton
3. Cephalic shield (dotted lines indicate relationship is undecided)
4. Carapace (extending posteriorly beyond cephalon), tergites lacking
5. Carapace bivalved
6. Telson processes (this character is almost certainly convergent and therefore invalid)
7. Distinction between thorax and abdomen
8. Paddle-shaped limbs in caudal furca
9. Incorporation of limbs (not antennae) into head posteriorly, reduced second antenna
10. Phyllocarid trunk segmentation
11. Tergites with pleurae following cephalic shield
12. Incorporation of limbs (not antennae) into head posteriorly
13. Two posterior cephalic limbs
14. Three posterior cephalic limbs
15. Unresolved
16. Fused posterior shield or pygidium
17. Loss of pre-telson appendages
18. Four posterior cephalic limbs, specialization of cephalic limbs distally, flat paddlelike telson
19. Unresolved
20. Loss of inner rami of trunk limbs

## 12. STRATIGRAPHIC AND DEPOSITIONAL SUMMARY OF MIDDLE AND UPPER CAMBRIAN STRATA IN NORTHEASTERN WASHINGTON, NORTHERN IDAHO, AND NORTHWESTERN MONTANA

By

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Measured sections of Middle and Upper Cambrian strata from Metaline Falls, Washington, Lakeview, Idaho, and the Libby Trough, Montana (fig. 1), are compared. Each measured section reveals a basal sand-shale succession overlain by upward-shallowing carbonates that are capped by algal dolostones. These carbonate successions are a vertical record of a transect across the seaward part of the middle carbonate belt of the Cambrian shelf and define large depositional cycles that formed during late Middle Cambrian time.

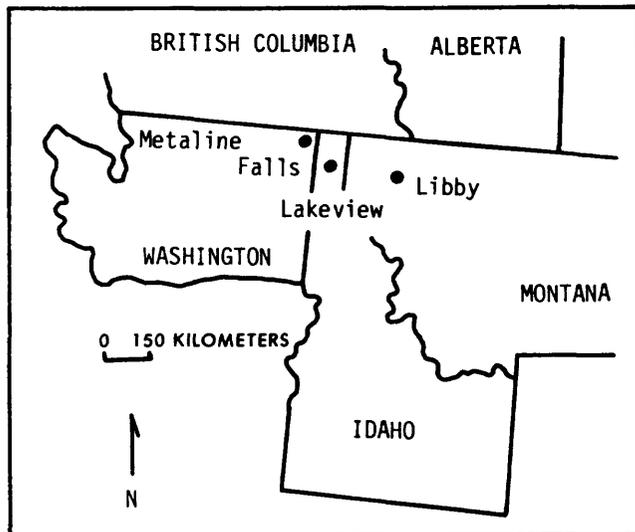


Figure 1.--Index map showing general location of study area.

Correlations of depositional cycles indicate that the edge of the shelf was located in what is now northeastern Washington, and that a large peritidal/algal-shoal complex existed on the outer edge of that shelf (Aitken, 1978; Bush and others, 1980; Martin and others, 1980). The carbonate complex was several hundred kilometers wide, and separated an outer, deeper basin in what is now northeastern Washington, from an inner basin in what is now central Montana. Development of the shoal complex

influenced sediment distribution, salinity, dolomitization, current activity, faunal distribution, evaporation, and tidal range during most of Middle and Late Cambrian time.

### NORTHEASTERN WASHINGTON

Cambrian strata crop out at many localities in Pend Oreille and Stevens Counties, northeastern Washington. In Pend Oreille County, near the town of Metaline Falls, the Cambrian section has been subdivided from base upward into the Gypsy Quartzite (1740-2790 m thick), Maitlen Phyllite (1250-1640 m thick), and the Metaline Formation (985-1250 m thick).

The Metaline traditionally has been subdivided into three mappable units. The lower member (290-390 m thick) consists of dark, subtidal lime mudstones and packstones containing trilobites of late Middle Cambrian age (Lochman-Balk, 1972). The middle member (360-390 m thick) consists of peritidal algal dolomudstones with associated subtidal units (Harbour, 1978). The upper member of the Metaline (196-450 m thick) consists of subtidal, bioturbated, lime mudstones and intraclastic packstones.

In addition to those three members, another member of the Metaline has been mapped as intraformational breccia by Yates (1964), referred to herein as the member at Fish Creek. Fischer (1980) described this unit and believed it to be a lateral equivalent of parts of the middle and upper members of the Metaline Formation. The member at Fish Creek (450 m thick) consists of black, thinly bedded dolomudstones interbedded with black and gray dolofloatstones. The dolomudstones are often finely laminated and contain black chert nodules. Dolofloatstones occur in 2- to 3-m-thick sedimentation units composed of poorly sorted, tabular clasts floating in black dolomicrite.

Overlying the Metaline Formation in northeastern Washington is the Lower Ordovician Ledbetter Formation, which consists mostly of dark-colored, basinal, siliciclastic mudstones. The contact between the Ledbetter and the Metaline varies from erosional to depositional at different localities (Hurley, 1980).

The lower and middle members of the Metaline represent an upward-shallowing sequence, with carbonate deposition controlled by upbuilding. In late Middle Cambrian time, local buildups coalesced and tidal flat sedimentation extended to the shelf edge where slumping caused semiconsolidated layers to move downslope producing the member at Fish Creek seaward of the shoal complex. A retreat of the shoal returned subtidal conditions to some areas and formed the limestones of the upper member of the Metaline.

The basin seaward of the shoal contained anoxic waters. Evidence for this condition is as follows:

1. The unusual abundance of dark-colored carbonates in the Metaline section.
2. The general lack of body fossils in subtidal limestones in the upper member of the Metaline.
3. The lack of fossils, and the presence of primary depositional laminae and black chert in the member at Fish Creek.
4. The occurrence of overlapping, dark, basinal, siliciclastic mudstones in the Ledbetter Formation.

#### NORTHERN IDAHO

Cambrian outcrops in northern Idaho are limited to small areas along the southern shores of Lake Pend Oreille where they are complexly faulted and locally metamorphosed. From base upward the sequence consists of the Gold Creek Quartzite (130 m thick), the Rennie Shale (30 m thick) and the Lakeview Limestone (600 m thick). The Lakeview is subdivided into a lower limestone member and an upper dolostone member.

The lower member of the Lakeview (360 m thick) contains fossiliferous, parallel-laminated, dark-colored lime mudstones at its base, that are overlain by sparsely fossiliferous, bioturbated, dark-colored lime mudstones. An assemblage of trilobites and brachiopods from the lower member of the Lakeview indicates a late Middle Cambrian age (Motzer, 1980).

The upper dolostone member of the Lakeview (240 m thick) can be subdivided into a pellet-packstone unit (30 m thick), a middle laminated mudstone unit (40 m thick), and an upper stromatolitic mudstone unit (170 m thick). The pellet-packstone unit consists of interbedded and repetitive units of light-colored pellet packstone, wackestone, and mudstone. Less abundant are concentrations of pisolithic, oolitic, intraclastic packstones and grainstones.

The laminated unit consists of brightly colored, alternately laminated, very dusky red-purple and grayish-green to white, finely crystalline dolomudstones. In addition to laminations, many sedimentary structures are present including microteepee structures, enterolithic folds, small nodules, coalesced nodules, cryptalgal features, algal stromatolites, mudcracks, fenestral fabric, and rare raindrop impressions.

The rocks of the stromatolitic mudstone unit consist of slightly metamorphosed, light-colored, stromatolitic dolomudstones. Recrystallization has destroyed most of the original textures, although "crinkly" laminae interpreted as flat-lying algal features can still be distinguished on weathered surfaces and polished slabs. No younger Paleozoic rocks have been identified in northern Idaho.

The Lakeview Limestone represents an upward-shallowing succession from subtidal carbonates in the lower member of the Lakeview to peritidal carbonates in the upper member of the Lakeview. This succession corresponds to the upward-shallowing cycle represented by the lower and middle members of the Metaline in northeastern Washington. The upper member of the Lakeview was part of the same shoal complex as the middle member of the Metaline, but at Lakeview the sedimentary structures indicate that subaerial exposure and high evaporation rates were common.

#### NORTHWESTERN MONTANA

In northwestern Montana, between the towns of Thompson Falls and Libby, Cambrian rocks are preserved in a northwest- to southwest-striking, downfaulted syncline referred to as the Libby Trough. The basal unit is the Flathead Quartzite (8 m thick) which is overlain by the Wolsey Formation (75 m thick). The Wolsey is overlain by an unnamed unit informally referred to as the Fishtrap dolomite (Aadland, 1979).

The Fishtrap dolomite has been subdivided by Aadland (1979) into a basal part consisting of a bioturbated mudstone unit (244 m thick), a dolomitized oolitic and pelloidal grainstone unit (61 m thick), and an algal dolomudstone unit (92 m thick). This succession is overlain by a light-colored shale unit (92 m thick) and an upper algal doloboundstone-dolomudstone unit (407 m thick). Overlying younger Paleozoic rocks have not been identified in the area.

The basal bioturbated mudstone, oolitic grainstone, and algal dolomudstone succession represents an upward-shallowing cycle similar to that represented by the Lakeview and the lower and middle members of the Metaline. Regional correlations by Aadland (1979) indicate that this cycle in the Libby Trough is late Middle Cambrian age. Together, the Lakeview, Metaline, and Libby Trough buildups formed extensive late Middle Cambrian shoals. In the Fishtrap dolomite, the shale unit represents a temporary decrease in the size of the carbonate-producing shoal, whereas the overlying algal dolostones represent a return to shoal conditions.

## DEPOSITIONAL MODEL AND RELATIONSHIP TO GRAND CYCLES

A four-stage depositional model explains the cycles discussed herein. Stage one begins with deposition on a gently sloping ramp with carbonates grading into clastics towards the land. Stage two began with carbonate upbuilding as clastic lithofacies transgressed towards the craton. Carbonates then built outward from a number of loci in late Middle Cambrian time, and eventually coalesced (stage three) into an extensive peritidal/algal-shoal complex that covered the entire area (Bush and others, 1980). In Late Cambrian time, the size of the complex was changed by varying progradational rates, that produced an intricate migrating mosaic of peritidal and subtidal environments (stage four).

Internal lithologic differences at each locality are the result of different paleogeographic positions within the shoal complex. In northeastern Washington, where the shoal was at the shelf edge, the succession grades seaward into slope deposits. The Metaline succession is modified vertically where transgressing, anoxic, basinal waters influenced the deposition of the subtidal carbonates of the upper member. At Lakeview, Idaho, evaporite features are more prevalent due to its central position on the crest of the shoal complex. In the Libby Trough, clastics interrupt the shallowing-upward cycle due to its proximity to the cratonic shoreline.

In Alberta, Aitken (1966, 1978) described two major types of Cambrian grand cycles referred to as the Stephen and Sullivan types. Stephen cycles formed during minimum shoal development and Sullivan cycles formed during maximum shoal expansion. Although they are upward-shallowing cycles, they do not correspond in sequential detail to the cycles in the study area. The Alberta counterparts contain less dolomite and more subtidal limestone. Both Stephen and Sullivan cycles were produced in the inner basin, whereas the cycles discussed herein were produced on the outer shelf edge within the shoal complex itself. The major difference in cycles between the two areas, therefore, relate to their different paleogeographic locations.

### IMPORTANCE OF SHOAL DEVELOPMENT

The peritidal/algal-shoal complex described herein was part of a much larger outer-shelf geographic feature that, according to Aitken (1978), extended from northern Alberta southward to at least the southwestern corner of Wyoming. Earlier, Aitken (1971) showed that parts of the shoal referred to as the "Kicking Horse Rim" in southwestern Canada controlled the distribution of sedimentary facies. At maximum shoal size, tidal exchange with the inner

basin would have been prevented, and at minimum shoal size, tidal exchange would have occurred through many small passes in the shoal (Aitken, 1978). The interpretations by Aitken (1971, 1978) help to explain facies differences within the Cambrian rocks of northeastern Washington, northern Idaho, and northwestern Montana.

Aitken (1978) stated that the shoal at its maximum development intersected the cratonic shoreline near what is now the Peace River Arch in northern Alberta, and controlled clastic facies distribution in the inner basin. In Utah, Robison (1976) stated that faunal exchange between nearshore sands and lagoonal muds and outer shelf muds was limited by shallow-water carbonate barriers during Middle Cambrian time. Lack of interchange with the outer basin also influenced salinity in the inner basin.

Early diagenetic dolomitization also can be related to shoal development. A sharp boundary presently exists between north-south striking Middle Cambrian limestone and dolostone lithofacies in western Montana. This boundary is readily visible on lithofacies maps for the *Bathyriscus-Elrathina* and *Bolaspidella* Zones presented by Lochman-Balk (1972). This boundary corresponds to the inner edge of the shoal complex. When the size of the shoal was extensive, maximum subaerial exposure and minimum exchange with the open sea existed. At this time, algae flourished, evaporator rates were high, and early penecontemporaneous dolomitization was extensive. At the same time, development of normal marine fauna and subtidal sedimentation would have been reduced. At its minimum development, the shoal would have had a "leaky" rim that would have allowed more exchange with basinal waters which in turn would have reduced the evaporation and algal growth and allowed wider distribution of normal marine fauna and subtidal sediments.

### SUMMARY

Upward-shallowing, late Middle Cambrian grand cycles at Metaline Falls, Lakeview, and in the Libby Trough document the development of a shoal complex at the outer shelf edge. Migration of the shoal and changes in its size influenced;

1. Evaporation, algal growth, and early penecontemporaneous dolomitization on the shoal complex.
2. Salinity and distribution of normal marine fauna in the inner basin.
3. Tidal range, current activity, and distribution of clastic lithofacies in the inner basin.
4. Vertical lithologic successions and depositional cycles on the shoal and in the inner basin.
5. Thickness and distribution of slope carbonates on the outer edge of the shelf.

The peritidal/algal-shoal complex described in this report was a major geomorphic feature on the Cambrian shelf. The shoal influenced regional sediment distribution during late Middle Cambrian time in what is now northeastern Washington, northern Idaho, and northwestern Montana.

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### 13. PRECAMBRIAN-CAMBRIAN BOUNDARY IN KOREA

By

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The occurrence of Protolenus in a thin shale unit near Pyeongyang City, North Korea, has been known for more than 50 years. The shale, about 10 m thick, is covered by Munsanri Quartzite and underlain by late Precambrian carbonate rocks of the so-called Sangweon System. Protolenus may indicate an age of middle Early Cambrian. In South Korea, no fossils from the basal part of the Cambrian System have been found. Near Jangseong in the northeastern part of South Korea, the Jangsan Formation, which is correlatable with the Munsanri Quartzite of North Korea, is underlain conformably by dark-gray fine-grained sandstone. This sandstone may be correlated with the Protolenus shale, but a search for fossils in it has been unsuccessful. The sandstone has a basal conglomerate 2-4 m thick and is underlain nonconformably by the Precambrian old granite or by gray granite gneiss.

A short distance east of the above mentioned place, the Myeonsan Formation rests on the Precambrian granite gneiss. The basal conglomerate of Myeonsan is 2 m thick. The Myeonsan is composed

of more than 70 graded beds. A typical graded unit is 20-30 centimeters thick and has a pebbly, coarse basal sandstone which is overlain by gray sandstone and dark-gray slate in that order. Protolenus or Redlichia were expected to be found, but considerable effort was expended in vain.

About 10 kilometers west of Jangseong, Cambrian strata rest on Precambrian metasediments of the Taebaegsan Formation, for which an exact date has not been obtained. The inclined metasediments are overlain unconformably by fine-grained metamorphosed sandstone without shale, and the basal conglomerate, about 20 cm thick, consists of large, well-rounded pebbles.

All the Cambrian rocks mentioned above are overlain by Middle and Upper Cambrian and Ordovician sediments. The Precambrian-Cambrian boundary in Korea is thus well defined by unconformities, but the exact age of the basal part of the Cambrian is known for only one place in North Korea. The age of the Precambrian igneous rocks is only known near Jangseong, where they are about 900 million years old. The Precambrian sediments are still undated.

## 14. THE BURGESS SHALE FAUNA AS A MID-CAMBRIAN COMMUNITY

By

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England

Speculation on the possible community structure of the Burgess Shale fauna will be of wider interest if it can be shown that the fauna is exceptional only in terms of conditions of fossilization, and not with respect to its original composition. Two lines of argument suggest that the Burgess Shale fauna may be taken as an approximate guide to the original diversity of at least some Cambrian assemblages that lived in a comparable biotope, that is, moderately deep water, muddy sediments, close to the boundary between the median carbonate and outer detrital belts.

1. Imagine that the extraordinary conditions of fossilization had not occurred in the Burgess Shale, so that only animals with shelly skeletons survived to be fossilized. The resulting assemblage would presumably consist of trilobites, monoplacophorans, hyolithids, brachiopods, rare echinoderms, and sponge spicules; all of these are components of many Cambrian faunas. It should also be noted that practically all the genera of this shelly assemblage, unlike most of the soft-bodied animals, have been found at numerous Cambrian localities. A comparison between this hypothetically impoverished Burgess Shale assemblage and another slightly younger Cambrian assemblage (upper Wheeler Shale, Middle Cambrian of Utah), using the Kolmogorov-Smirnov test showed that there was no significant difference between the relative proportions of shelly groups in terms of genera (Conway Morris and Robison, 1981).

2. The second line of evidence suggesting that the Burgess Shale is a representative Cambrian community is the scattered occurrence of soft-bodied and lightly skeletonized fossils in other Cambrian rocks. In some cases these fossils are cogenetic with Burgess Shale forms, but more often they represent unique records. This distribution of soft-bodied and lightly skeletonized species may indicate that they played an important role in some Cambrian communities.

### STATUS OF KNOWLEDGE

Recent work has emphasized the detailed morphology, together with some functional morphology, of many of the species. The overall structure of the fauna has received less attention,

although estimates of the composition and major ecological groupings in terms of genera have been available for several years (Conway Morris, 1977, 1979). In this report the total of 120 genera (mostly monospecific, species total about 150) from the Walcott Quarry, including genera known only from carapaces or other resistant skeletal remains, has the following distribution (figures in percent): arthropods 37.4, miscellaneous genera 16.6, sponges 15.1, lophophorates (mostly brachiopods) 6, priapulids 5, polychaetes 5, echinoderms 4.2, molluscs (including hyolithids) 3.3, cnidarians 3.3, hemichordates 2.5, and chordates 1.6. These figures differ little from earlier compilations.

In an attempt to answer questions and problems relating both to the ecology of the Burgess Shale fauna and its relationships to other Cambrian assemblages it was decided to prepare specimen counts which would give information on the relative importance of individuals and, by simple calculations, on biovolumes. As the average length of genera may differ from a few millimeters to over 300 mm, biovolumes may be a more useful guide to relative ecological importance.

### METHODS

The basic data of specimen counts and distribution of species on collected slabs comes from two principal sources. The most important is Walcott's very large collection in the Smithsonian Institution's Museum of Natural History (formerly the United States National Museum, USNM), Washington, D.C. The second source is a smaller collection made by the Geological Survey of Canada (GSC) in 1966 and 1967. In addition to these collections several museums and universities possess minor holdings of Burgess Shale material. In most cases these small collections were acquired through exchanges with the USNM, and they are treated as part of the major USNM holding.

Burgess Shale specimens occur as parts and counterparts. A serious problem with the USNM collection is that in only about 3 percent of instances are part and counterpart associated. For the remaining specimens, either the part and counterpart are stored in separate drawers or the counterpart was

never collected. On the basis of several species where the total of parts and counterparts is known, it is estimated that about 75 percent of unassociated specimens are only known from the part, while 25 percent consist of disassociated parts and counterparts. Collectors for the GSC made it a point to keep together parts and counterparts. A survey of the collection, however, suggests that some diassociation of parts and counterparts has inadvertently occurred. In 66 percent of instances where only the part is known it is assumed that the counterpart was not collected, but in the remaining 34 percent of instances disassociation is presumed to have occurred. If these figures are accepted the original proportion of GSC specimens consisting of part and counterpart was about 46 percent.

Using these correcting factors for the USNM and GSC collections, it is estimated that the available fauna consists of about 73,250 specimens (including animals, algae, and indeterminate forms), occurring on about 30,000 slabs of rock (parts only and parts plus counterparts). The remainder of this report deals only with the animal component (estimated 64,357 specimens) and in particular with that fraction that is judged to have been alive at the time of burial (estimated 40,375 specimens).

#### INDIVIDUALS AND BIOVOLUMES

In terms of individuals (alive and dead at time of burial) the Burgess Shale animals have the following distribution (figures in percent): arthropods 57.6, mollusks 14.7, hemichordates 14.5, priapulids 4.35, lophophorates (mostly brachiopods) 2.5, sponges 2.45, echinoderms 1.25, polychaetes 0.9, miscellaneous genera 0.45, cnidarians 0.2, and chordates 0.1, while the remaining 1 percent of specimens were indeterminate. For paleoecological purposes, however, it is appropriate to distinguish between dead specimens, which persist in the community by virtue of their resistant skeletons, and those living at the time of burial. All animals with evident soft or lightly skeletonized parts are interpreted as having been alive immediately prior to burial. In the case of some animals with hard parts, distinguishing live specimens from dead ones is possible even when the soft tissue itself is not apparent. In Hyolithes (Hyolitha) the presence of attached helens and opercula is good evidence for vitality, while in Dictyonina (Inarticulata) the presence of mantle setae protruding from the valves is similarly interpreted as evidence of specimens having been alive at burial. In monoplacophorans, such as Scenella, and in most brachiopods such criteria are not available, so the proportion of live to dead individuals is arbitrarily taken to be the same as for Hyolithes (5 percent for mollusks) and Dictyonina (14 percent for

brachiopods). It appears that the specimens alive at the time of burial show the following distribution (in percent): arthropods 60.8, hemichordates 23.2, priapulids 4.5, sponges 3.8, echinoderms 2, polychaetes 1.4, mollusks 1.4, lophophorates (mostly brachiopods) 0.6, miscellaneous 0.4, cnidarians 0.3, and chordates 0.2, while the remaining 1.4 percent of individuals are indeterminate.

The overall composition of the fauna was also assessed in terms of biovolumes, which were calculated for each genus (mostly monospecific) judged to have had living representatives at the time of burial. In terms of biovolume the fauna may be characterized as follows (in percent): arthropods 50, sponges 16.5, echinoderms 15.3, priapulids 9.9, cnidarians 4.3, hemichordates 1.0, miscellaneous genera 0.7, mollusks 0.7, polychaetes 0.2, lophophorates (mostly brachiopods) 0.05, and chordates 0.01, with the remaining 1.3 percent belonging to indeterminate specimens. The number of individuals and biovolumes of the genera within three phyla (arthropods, priapulids and polychaetes) are considered in more detail. With priapulids and polychaetes the relative abundance of individuals matches the relative biovolume for each monospecific genus fairly well. In the arthropods, however, there are major discrepancies, because small, abundant arthropods are rivalled in biovolume by much rarer but larger arthropods.

#### ECOLOGY

The ecology of the fauna is considered in terms of two broadly defined parameters: habitat (sessile and vagrant infauna, sessile and vagrant epifauna, nektobenthos, and pelagic floaters and swimmers) and feeding type (high- and low-level suspension, deposit collectors and swallowers, predators and scavengers, and unknown). The relative importance of habitats and feeding type is considered in terms of number of genera, number of individuals, and biovolumes. The dominant phylum within each habitat and feeding type is identified. The entire benthic community is dominated by the epifauna in terms of genera, individuals and biovolumes. The vagrant epifauna consists largely of arthropods, while the sessile epifauna is dominated by sponges. The pattern of distribution within benthic feeding types is more complex. In terms of individuals, deposit feeders predominate, with suspension feeders ranking an important second. With regards to biovolume, however, there is a more nearly equal distribution of feeding types with predators and scavengers apparently accounting for more than 30 percent of the total biovolume. A more detailed synthesis of the trophic structure of the Burgess Shale community, including a reconstruction of food webs and trophic

pyramids and an assessment of the relative importance of trophic levels, is difficult because of uncertainty regarding the precise feeding habits of many species.

#### GENUS FREQUENCY RELATIONS

The pattern of genus frequency distributions in terms of both individuals and biovolumes has also been examined, principally by plotting dominance-diversity curves, in which the log of relative importance is plotted against genus rank from most abundant to rarest. The resulting curves are used widely in ecological work and occasionally by palaeontologists, as in McBride's (1976) study of Late Cambrian communities. Several standard types of curves have been recognized in the literature and may be related to hypotheses concerning niche distributions. For the Burgess Shale fauna, dominance-diversity curves have been prepared for groups whose members might be expected to have had some overlap in their niches. The possible significance of these results will be addressed.

#### INTER-GENERIC RELATIONS

The transport of the fauna by debris flows and the intermixing of genera that occupied distinct habitats, combined with the dissection of the fossil collections into thousands of small sawn slabs, could cause some difficulty in finding ecologically significant associations or disassociations.

Nevertheless, the overall distance of transport appears to have been small, and the lack of abrasion or breakage suggests that transport was not especially turbulent. In an attempt to see if any patterns emerged that might be related ultimately to factors such as competition, all associations on the collected slabs were recorded.

#### CONCLUSIONS

At the time this report was prepared, various lines of enquiry were still incomplete, but the project should be substantially completed by July 1981. The Cambrian Symposium at Golden, will therefore, provide an opportunity for a broad review of the community structure of the Burgess Shale fauna and will allow some speculations on its place in Cambrian life.

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## 15. LATE CAMBRIAN-EARLY ORDOVICIAN CONTINENTAL MARGIN SEDIMENTATION, CENTRAL NEVADA

By

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Lower Paleozoic rocks in the Great Basin of the western United States reflect a broad continental shelf to the east and either a marginal ocean-basin and volcanic-arc system (Burchfiel and Davis, 1972; Churkin, 1974) or an open-ocean basin to the west (fig. 1) (Dietz and Holden, 1966; Stewart, 1972; Stewart and Poole, 1974; Stewart and Suczek, 1977).

Upper Cambrian and lowermost Ordovician marine carbonate rocks in the Egan Range (Whipple Cave Formation and lower House Limestone) and the Hot Creek Range (Hales Limestone and lower Goodwin Limestone) of Nevada show that the Egan Range section represents shoal-water deposition on a shallow carbonate shelf whereas, 170 km to the west, coeval limestone in the Hot Creek Range was deposited on a continental shelf margin, slope, and rise (fig. 2). The sedimentary record and stratigraphic succession, from the base of each section upward, records a progressive shallowing of water that reflects a westward progradation of the continental shelf and slope (Cook and Taylor, 1975, 1977; Taylor, 1976, 1977; Taylor and Cook, 1976; Cook and Chamberlain, 1978). Thus, at least by Late Cambrian time a sinuous, but overall north-trending continental margin existed in central Nevada (fig. 1) (Taylor and Cook, 1976; Cook and Taylor, 1977; Rowell and others, 1979). It should be pointed out, however, that the influence of post-depositional tectonics on the shape of the margin is still poorly understood. This becomes especially pertinent when trying to evaluate possible local meanderings of the margin.

### CONTINENTAL MARGIN DEPOSITS

The ancient continental margin of western North America is considered to have formed when a rift and spreading center developed within the continent and the fragments drifted apart forming a new ocean basin: the Pacific (fig. 3) (Stewart and Suczek, 1977). We propose that a deep ocean-margin basin existed by Late Cambrian time and that the 1,500+ m of seaward prograding basin plain, fan, and slope deposits in the Hot Creek Range started to accumulate in water depths 1,500 m or more. The resulting depositional facies consist of a deep-water basin-plain sequence of laminated hemipelagic limestones, argillaceous limestones, and thin-bedded cherts and turbidites represented by the Swarbrick Formation and lower

Dunderberg Shale (fig. 4). This is gradationally overlain by a wide variety of carbonate-turbidite and debris-flow deposits whose facies collectively form a submarine fan represented by the uppermost Dunderberg Shale and lower Hales Limestone (Cook and Egbert, 1981). The submarine fan facies, in turn, grade upward into submarine slide, slump, and contourite deposits that formed on the continental slope (upper Hales Limestone). The uppermost part of the sequence (uppermost Hales Limestone and lowermost Goodwin Limestone) appears to have been deposited on or near the shelf margin. Thus, the 1,500+ m of ocean-margin basinal relief was gradually reduced as continental margin sediments prograded to the west (seaward).

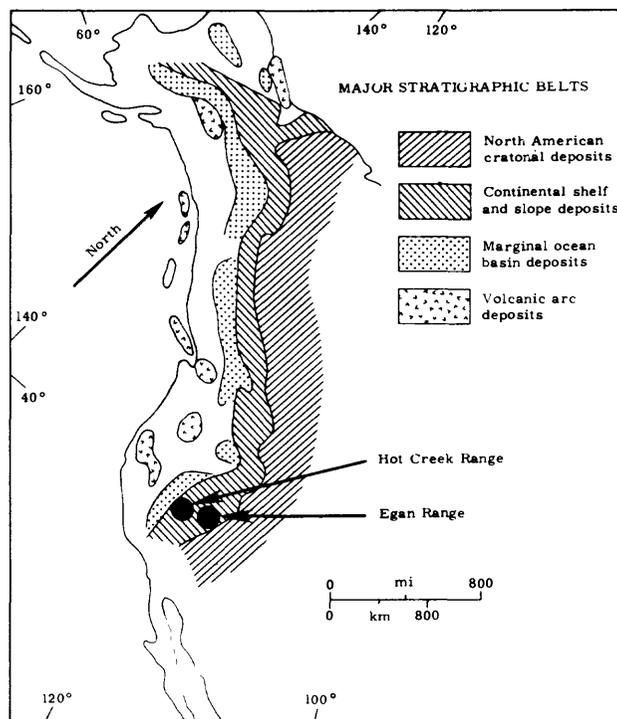


Figure 1.--General location of sections in the Hot Creek Range and central Egan Range, Nevada, in relation to major regional stratigraphic belts (from Taylor and Cook, 1976; map generalized from Churkin, 1974).

The focus of this paper is on the slope and submarine-fan deposits (upper Dunderberg Shale and Hales Limestone).

Slope Facies (about 250 m thick): The upper-slope sequence consists mainly of light-gray hemipelagic and periplatform lime mudstones and packstones derived from the shelf. Transport of this material from the shelf onto the slope was probably by tidal and seasonal currents and storms. The upper slope sediments are further characterized by their medium-bedded nature and the presence of horizontal burrows. Thin-bedded turbidites, whose constituents were mainly derived from the shelf, are also common to the upper slope; debris-flow deposits are less abundant. An important and unique facies, apparently restricted to the slope, is well-sorted, rippled contourite deposits.

Facies in the lower slope sequence are distinctly different from the upper slope facies in that in-situ lower slope deposits are finer grained and darker in color. They consist of black hemipelagic and periplatform lime mudstones and abundant mass transport deposits. In-situ pelagic and hemipelagic sediment is thin-bedded, contains millimeter-thick laminae, and is virtually devoid of burrows. The associated fauna consists of sponge spicules and deep-water cosmopolitan trilobites (Cook and Taylor, 1975, 1977; Taylor, 1976, 1977; Taylor and Cook, 1976).

Mass-transport deposits in the lower slope sequence include abundant slides and slumps up to 10 m thick and 400 m wide. The slumps were generated on the lower slope from semiconsolidated

dark lime muds. Some slides moved downslope into base of slope and rise settings with very little internal deformation. Other slides are intensely deformed and were completely remolded into conglomeratic debris flows and turbidity flows yielding large volumes of debris that contributed to form the submarine fan facies (fig. 4) (Cook, 1979a, 1979b; Cook and Egbert, 1981).

Carbonate Submarine Fan Facies (about 250 m thick): The literature lacks examples of carbonate sediment gravity-flow deposits whose facies can be described by clastic submarine-fan models (Cook and Egbert, 1981). Mass-transport deposits, though common in carbonate basins throughout the geologic column, normally occur as widespread sheets or debris wedges, as in the Devonian of Canada and elsewhere (Cook and others, 1972; Mountjoy and others, 1972; Johns and others, 1981; Cook and Mullins, 1981) or in modern intraplatform troughs such as in the Bahamas (Schlager and Chermak, 1979; Crevello and Schlager, 1980; Cook and Mullins, 1981).

The inner fan facies are considered to have been deposited on the lower-most slope and adjacent basin (fig. 4) and are characterized by submarine slides and several entrenched feeder channels 10 m deep and 500 m wide. The channels are filled with disorganized boulder-bearing conglomerates and megabreccias (Cook and others, 1972, p. 443); but are not arranged in any well-defined thinning- and fining-upward sequences.

Stratigraphically below the inner fan feeder-channel deposits is a facies interpreted to represent braided mid-fan distributary channels (fig. 4). This facies consists of thinning- and fining-upward organized pebble- to cobble-bearing channelized conglomerates and thin-bedded turbidites. The channels are 1-5 m deep, 20-100 m wide, and rapidly coalesce laterally and vertically. The conglomerates grade laterally into and are interbedded with thin and discontinuously bedded ripple-laminated and graded calcarenites, similar to submarine fan, overbank-levee, and interchannel deposits (Cook and Egbert, 1981). The mid-fan distributary-channel system has a minimum lateral width of 1.5 km.

Below the braided channels are thickened- and coarsened-upward cycles of virtually nonchannelized beds; beds in the cycles are composed of calcarenites exhibiting Bouma divisions  $T_{a-e}$ ,  $T_{abe}$ ,  $T_{ae}$ ,  $T_{ce}$ . These carbonate sands are interpreted to represent prograding outer fan lobes (fig. 4).

Pelagic and hemipelagic sediment in the basal Hales and upper Dunderberg sharply contrast in color. A change from black laminated sediment in the Hales to lighter colored olive-gray and tan beds in the Dunderberg is relatively abrupt and occurs over a thin (about 5 m) transitional interval where in-situ lithologies of the two formations are interbedded.

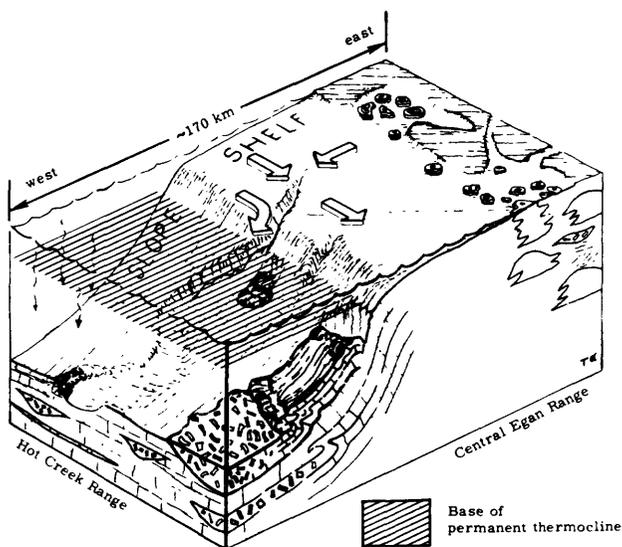


Figure 2.--Graphic model of inferred shelf-slope-rise transition in the Late Cambrian and earliest Ordovician of Nevada. Not to scale (modified from Cook and Taylor, 1975; drawn by Tau R. Alpha).

Although the distinct color differences serve to define a mappable boundary between the formations, the upper 50-75 m of the Dunderberg Shale has a few thickening- and coarsening-upward turbidite cycles (Bouma  $T_{be}$ ,  $T_{bce}$  divisions) similar to the lowermost part of the Hales Limestone. Thus, the upper part of the Dunderberg Shale appears to represent the outermost fringe of prograding fan lobes (fig. 4).

**Basin-Plain Facies (about 1000 m thick):** The remainder of the Dunderberg Shale, stratigraphically below the outer fan-fringe sediments, consists mainly of fine-grained hemipelagic argillaceous lime mudstones and limey shales. Thin-bedded turbidites are present in the lower Dunderberg but they are not as abundant as in the upper Dunderberg.

The contact between the Dunderberg Shale and the underlying Swarbrick Formation is structurally complex but depositional contacts can be found. At the contact, thin-bedded turbidites that display flute and tool marks, as well as horizontal burrows, are common. Turbidites within the lowermost Dunderberg Shale are very fine grained, exhibit only Bouma  $T_{bcde}$ ,  $T_{cde}$ , and  $T_{de}$  divisions, are thin bedded (2-5 cm), and are not associated with any other types of sediment gravity-flow deposits. They probably represent distal basin-plain turbidites.

The two lithologies that characterize the Swarbrick Formation consist of a gray, thinly laminated lime mudstones and an interbedded black laminated chert. Both lithologies occur in laterally continuous beds only a few centimeters thick. It is not certain whether the laminated lime mudstones in this deep basin-plain setting are dilute turbidites exhibiting only Bouma  $T_{de}$  divisions or whether they originated as pelagic deposits. Both types of lime mudstones may be present. The chert, however, contains remnants of sponge spicules and this facies and its contained benthonic fauna are considered to have originally formed in a deep-water setting.

**DEPOSITIONAL SETTING: CONTINENTAL SLOPE AND OCEANIC BASIN OR CONTINENTAL-SHELF BASIN?**

It has been suggested that the rocks described above and partly coeval rocks in northern Nevada may have formed in a deep basin on the outer continental shelf (Rowell and Rees, 1980; Rowell and Rees, this volume) rather than on the continental margin of the western United States (Cook and Taylor, 1975, 1977; Taylor and Cook, 1976). Rowell and Rees propose that the true continental slope was farther to the west. It is beyond the scope of this paper to rigorously evaluate each possibility. We do, however, offer various lines of evidence that lead us to favor a continental slope and adjacent open ocean or large marginal ocean basin for the origin of these rocks.

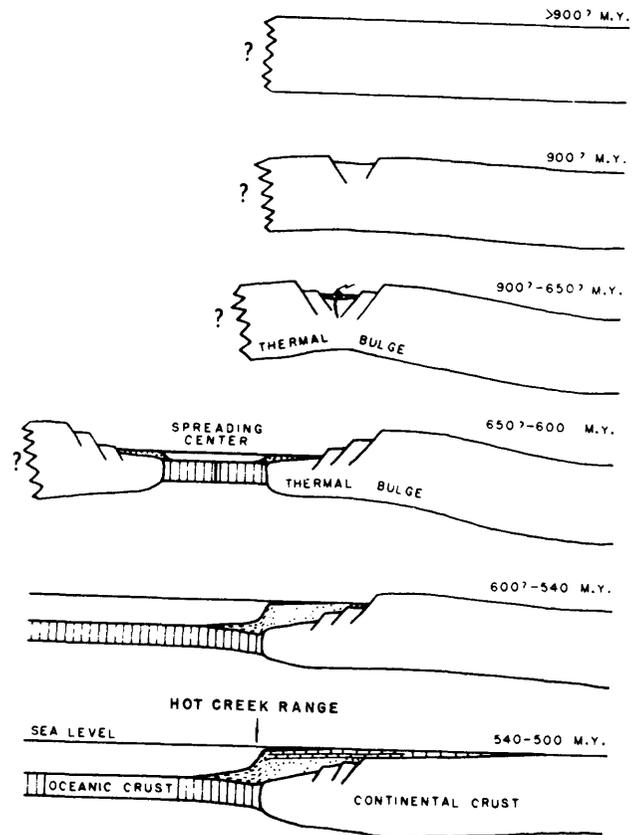


Figure 3.--Diagram showing a model of the late Precambrian and Cambrian development of the western United States (modified from Stewart and Suczek, 1977).

We propose the following attributes for this basin. The debris and turbidity-current deposits were transported to the west. Initial water depths may have exceeded 1,500 m. The basin was large and contained a source of freely circulating water that included contour-flowing currents. Water in the basin was well oxygenated at the surface, had a thermocline, and contained an underlying oxygen minimum zone. Horizontal circulation existed beneath the oxygen minimum waters so that sediments in the deepest part of the basin accumulated in oxygen-rich waters.

**Source of Sediment Gravity Flow Deposits:** A deep basin on the outer continental shelf, as suggested by Rowell and Rees (this volume), implies that someplace to the west of the Hot Creek Range a mirror-image sequence of carbonates similar to the sequence shown in figure 4 could be expected. It also is implicit to an outer shelf-basin theory that carbonate sequences representing the true continental margin, slope, and oceanic basin were still farther to the west. To our knowledge, no such depositional sequence of carbonate rocks of this age have yet been documented in western Nevada.

Abundant paleocurrent data in the Hot Creek section, from debris-flow and turbidity-current deposits and submarine slides and slumps, indicate transport directions towards the west. If these deposits formed in an outer-shelf basin, one could expect to find turbidites derived from both sides of the basin. However, no paleocurrent data indicating a westerly source for the mass-transport deposits have been found. Certainly modern carbonate turbidites are capable of traveling at least 100 km (Schlager and Chermak, 1979; Crevello and Schlager, 1980; Cook and Mullins, 1981), and modern debris flows off the coast of the Spanish Sahara have traveled several hundred kilometers across basinal gradients as low as 0.1° (Embley, 1976). Furthermore, ancient carbonate debris flows and turbidity currents are capable of traveling long distances across gradients of a degree or less (Cook and others, 1972).

**Water Depths:** Modern basins on continental shelves are rarely deep. However, one deep continental-shelf basin off the coast of Venezuela has been studied in some detail and is discussed below under "Nature of the Water Column." Some very small basins on the Alaskan shelf, about 2 x 2 km in size, have water depths up to 75-100 m greater than the surrounding shelf (M. A. Hampton, oral commun., 1981). Even these are unusual as most continental shelves have only a few meters of relief, which is generally of depositional origin (M. E. Field, oral commun., 1981).

The gradual upward change in lithofacies from basin plain to submarine fan to slope and finally to relatively shallow-water shelf-margin carbonates supports our premise that initial sedimentation took place in deep water (fig. 4). We propose that water depths were on the order of 1,500+ m or equal to the thickness of the seaward-prograding, shallowing-upward section. Alternatively, water depths were at least deep enough to develop a permanent thermocline, an underlying oxygen-minimum zone, and a still deeper well oxygenated zone. Furthermore, a water depth of 1,500+ m does not take into account any calculations for compaction or for water depths at the shelf-slope break. Both of these factors would add to the initial depth below sea level on the basin plain. The use of sediment thickness as an approximation of water depth and (or) subsidence has been discussed and used by a number of geologists; for example, Kay (1945, 1955), Krumbein and Sloss (1963), and Benedict and Walker (1978).

The vertical lithofacies types, systematic depositional patterns (fig. 4), and nature of the water column strongly suggest that these rocks did not accumulate in a shallow low-relief basin with sedimentation simply keeping pace with basin subsidence.

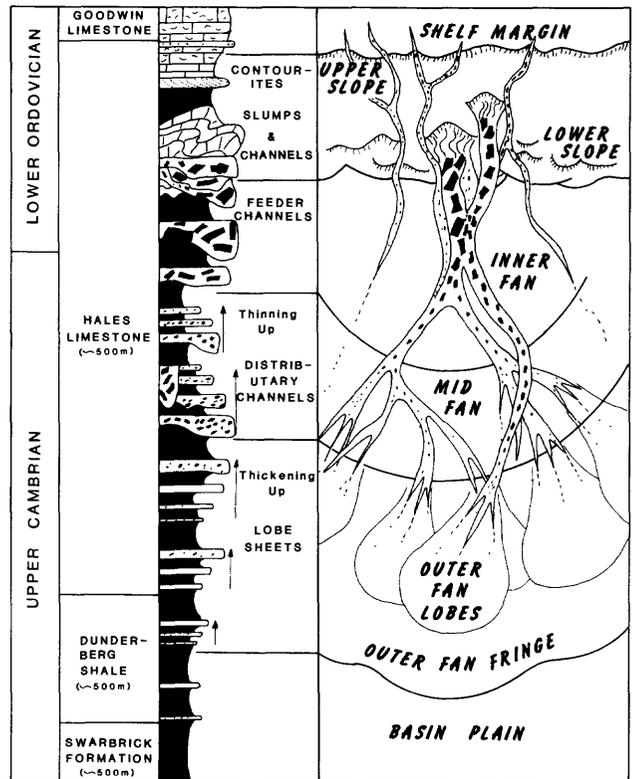


Figure 4.--Carbonate slope, submarine-fan, basin-plain model relating formations to depositional environments and facies, Hot Creek Range, central Nevada, western United States. See text for thicknesses and descriptions of depositional facies. No relative scales implied.

**Contour Currents and Basin Size:** Within the slope sequence is an interval of numerous 2-cm-thick lime calcarenite beds interbedded with in-situ black laminated pelagic lime mudstones. The calcarenites have grainstone fabrics, are laminated, have foreset bedding and ripple forms, and have sharp lower and upper contacts with the enclosing dark lime mudstones (Cook and Taylor, 1977). The calcarenites consist mainly of shoal-water derived *Nuia* (calcareous green alga) grains and lesser amounts of echinoderm and quartz particles. The grains are well sorted and have virtually no interparticle mud matrix. Ripple forms have about 0.5-cm heights and 9-cm wavelengths. The grain size of the sediments is about 0.25-0.1 mm in diameter (fine-sand size).

Paleocurrent data from the current ripples indicate a northerly current direction parallel to the paleoslope (that is, approximately perpendicular to the paleocurrent data on the mass transport deposits). As pointed out previously by Cook and Taylor (1977), the rippled calcarenites do not appear to be the product of

muddy turbidity currents. A different origin is indicated by the near-perfect hydraulic sorting, sharp lower and upper contacts, laterally continuous evenly spaced current ripples, and transport direction parallel to the slope. The sediments are most likely the result of winnowing of previously resedimented material by strong bottom-hugging contour currents. Similar limestone beds deposited on a Cretaceous continental slope have been ascribed a contourite origin (Bein and Weiler, 1976).

To initiate movement of grains in the 0.25-0.10 mm grain size and to produce ripples requires bottom currents on the order of 15 cm/s and greater (Shepard, 1973). Modern ocean-floor currents can result from (1) prevailing winds, which produce permanent-flowing gyral currents, (2) tidal forces that cause fluctuating currents, and (3) thermohaline currents due to differences of water density (Shepard, 1973). Permanent ocean-floor currents along the continental margin of the western United States have velocities of as much as 20 cm/s (M. E. Field, oral commun., 1981) and thermohaline currents in the Atlantic have reported velocities of as much as 50 cm/s (Bouma and Hollister, 1973). Except in restricted passages and very large basins, tidal currents normally do not exceed a few centimeters per second and would be expected to flow up and down the slope, not parallel to the slope. In addition, periodic storm-driven bottom currents have low velocities in water deeper than about 50 m (Shepard, 1973).

Paleocurrent measurements in the rippled calcarenite beds indicate a fairly consistent northerly bottom-current direction parallel to the slope through time. This favors some uniform, fairly high velocity process such as a permanent ocean-floor current related to major oceanic-current gyres or thermohaline currents. Clearly, strong bottom-flowing contour currents are much more likely to occur in large marginal-ocean basins or open oceans than in deep relatively small basin on a continental shelf.

Nature of the Water Column: In modern open oceans, such as the western Pacific (Knauss, 1963; Sverdrup and others, 1973), the base of the thermocline approximately coincides with the top of the oxygen-minimum zone. Below the oxygen-minimum zone the waters once again are high in oxygen. Thus, there are three water layers--(1) an upper well-oxygenated layer due to surface mixing by waves and currents, (2) a stable oxygen-minimum zone below the thermocline, and (3) a deeper water oxygen-rich layer, the product of dense oxygen-rich bottom currents that originate at high latitudes and flow along the ocean floor toward the equator.

The nature of the sediments in the Hot Creek Range indicate that they formed in a basin whose surface waters were well oxygenated. Waters at intermediate depths contained an oxygen-minimum zone, and the deepest waters were once again oxygen

rich. This type of water column occurs in modern open oceans, however, this is not the case for deep basins on continental shelves where the oxygen-minimum zone extends to the base of the water column.

An important point to remember in any basin analysis is that in modern open-ocean basins there is horizontal circulation in both the upper and deepest parts of the water column. This results in the upper and lower water masses being well oxygenated and being separated by a fairly stable oxygen-minimum zone. In a deep continental-shelf basin, such as proposed by Rowell and Rees (this volume), horizontal circulation would probably be limited to the upper part of the water column. Circulation of water below the upper horizontally circulating waters can only take place by vertical-eddy diffusion (Redfield and others, 1963), which results in a stagnant continental-shelf basin.

The Cariaco Basin, described by Richards and Vaccaro (1956), Redfield and others (1963), and Edgar and others (1973), is an example of such a deep continental-shelf basin. It is a depression about 1,400 m deep on the continental shelf of Venezuela. The basin is oriented parallel to the trend of the shelf and is about 200 km long and 70 km wide, a size comparable to the shelf basin proposed by Rowell and Rees (this volume). Water depths on the shelf surrounding the Cariaco Basin are about 150 m (the basin's sill depth). Within the basin below 250 m water depth, the temperature and salinity are uniform and demonstrate that the water is isolated from the Caribbean water of comparable depths and can exchange with its surroundings only by vertical-eddy diffusion (Redfield and others, 1963). The result is that the waters in the basin are anaerobic below 350 m (Edgar and others, 1973). Bottom sediments contain abundant pyrite (Fan and others, 1973), have a hydrogen sulfide smell, are rich in organic matter, and are laminated (Edgar and others, 1973).

The slope-submarine-fan-basin plain sequence in the Hot Creek Range exhibits features that indicate an oxygen-minimum layer existed, but it was overlain and underlain by well-oxygenated waters. The upper part of the slope sequence is light gray in color and contains abundant evidence of burrowing. This sequence was probably deposited above the base of the thermocline and well within the upper well-oxygenated few hundred meters of the water column. Lower slope mudstones and in-situ hemipelagic mudstones interbedded with the submarine-fan turbidites are dark black, finely laminated, contain abundant pyrite, and lack apparent burrows. These sediments probably accumulated where the top and bottom of the oxygen-minimum zone intersected the slope and basin plain, respectively. The deeper water fan fringe and basin-plain deposits are light in color and once again exhibit horizontal burrows. These deposits probably formed below an oxygen-minimum zone in the deep well-oxygenated part of the water column where horizontal

circulation was active.

If the Hot Creek section had formed in a deep basin on the continental shelf, similar to the Cariaco Basin, it is likely that the entire lower part of the section below the upper well-oxygenated slope deposits would have formed in oxygen-minimum or anaerobic waters. The sediment and faunal evidence does not support such a stagnant type of basin.

#### SUMMARY

We propose that the 1,500-m-thick sequence in the Hot Creek Range formed on the continental margin in an open ocean or large marginal ocean basin setting. Water depths were deep and ranged from about 1,000-1,500 m or more for the basin-plain sediments to depths on the order of 100 m for the upper slope/shelf-margin deposits.

A deep-water basin on the continental shelf is an unlikely setting for these deposits because paleocurrent data from sediment gravity-flow deposits indicate (1) a westerly transport direction, (2) relatively strong northerly directed contour currents paralleling the basin slope, and (3) the water column was well circulated with oxygen rich waters in the surface and floor of the basin, with only intermediate water depths containing an oxygen-minimum layer.

Strong bottom-hugging contour currents and well-circulated waters in the upper and basal parts of the water mass, resulting from horizontal circulation, are characteristic features of water on modern continental slopes and ocean basins. These attributes are unlikely to occur in water of deep continental-shelf basins. In addition, not only are deep shelf basins rare, at least on modern continental shelves, but when they do occur, such as the Cariaco Basin, their waters are stagnant below a few hundred meters.

In spite of the fact that palinspastic reconstructions are uncertain, the regional trend of the early Paleozoic continental margin of western North America roughly parallels the modern Pacific continental margin. Locally, the trend of the Late Cambrian continental margin through Nevada may have been sinuous, as suggested by the geographic position of some basin-plain sequences. Even if these basin-plain sequences are in their original relative geographic locations, which is uncertain, sinuosity could be expected. Local sinuosity is normal along segments of modern continental margins the world over, and along ancient margins such as the Devonian of Canada and the Yukon Territory (Cook and others, 1972, fig. 1).

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## 16. UPPER CAMBRIAN DEPOSITIONAL ENVIRONMENTS, SOUTHEASTERN CALIFORNIA AND SOUTHERN NEVADA

By

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In recent years, a number of studies have focused on Middle and Late Cambrian regional paleoenvironmental patterns and paleogeography in parts of Nevada and Utah (Palmer, 1960; Kepper, 1972, 1976; Cook and Taylor, 1975; Koepnick, 1976; Lohman, 1976). Most significantly, this work has: (1) identified and detailed aspects of inner detrital, middle carbonate, and outer detrital belt lithosomes; (2) documented shelf-slope-basin transitions; and (3) described paleoenvironmental patterns and trends along a major part of the Late Cambrian transition between the Cordilleran craton margin and miogeoclinal shelf.

Little work of this nature has been published on areas in the southern Great Basin. However, regional stratigraphic subdivision of the Nopah Formation (Christiansen and Barnes, 1966; Barnes and Christiansen, 1967) in southern Nevada, and the Goodsprings Dolomite of the Goodsprings district, Nevada-California (Gans, 1974) has clearly identified stratigraphic units that can be correlated over a sizable area, thus facilitating regional stratigraphic analysis.

This report is concerned with the stratigraphic interval comprising the Dunderberg Shale and Halfpint Members of Late Cambrian age (Dresbachian-Franconian ages) of the Nopah Formation in an area along the California-Nevada border (fig. 1). This thin interval (the Dunderberg Shale Member ranges from 3 to 45 m thick and the Halfpint Member ranges from 20 to 65 m thick) is sandwiched between the thick carbonate units of the underlying Bonanza King Formation and the overlying Smoky Member of Late Cambrian and Early Ordovician age of the Nopah Formation. Distinctive lithologies, well-preserved depositional textures, fabrics, and structures, and locally abundant fossils make the Dunderberg-Halfpint succession especially amenable to an environmental stratigraphic study. Thirty-one measured sections (fig. 1) provide the control for determining the nature and distribution of lithofacies and stratigraphic cycles (fig. 2) and interpretation of depositional environments and paleogeography (fig. 3) for a short time interval during the Late Cambrian.

### LITHOFACIES AND PALEOENVIRONMENTS

Seven distinct lithofacies make up the Dunderberg-Halfpint interval. These are stromatolitic boundstone (I), thrombolitic boundstone (II), pelmatozoan calcarenite (III), oncologic limestone (IV), oolite (V), calcilitite containing intercalated siltstone and calcarenite-calcirudite (VI), and shale containing intercalated carbonates (VII). These lithofacies and their chief characteristics and general geographic and stratigraphic distribution, as well as interpreted depositional conditions and environments, are discussed below.

Lithofacies I--Stromatolites, confined to a few measured sections in the eastern part of the study area in Halfpint Member, are low relief, laterally linked, and crinkly mat forms. These morphologies, together with associated channels containing eocrinoid debris, some fenestral fabric, and small-scale lithologic cycles grading upward from algal mat to dessicated mat to algal rip-up clasts and skeletal debris, suggest intertidal to supratidal hypersaline conditions (Logan and others, 1974; Hoffman, 1976; Playford and Cockbain, 1976). The stromatolites were part of a major algal carbonate buildup but were confined mainly to the more massive, cratonward part of the algal bank complex.

Lithofacies II--Crinkly mat and domal thrombolites are most common in measured sections in the eastern part of the study area and a few central sections within the Halfpint Member; geographic and stratigraphic relations suggest most of the thrombolites formed in a belt seaward of the stromatolites. The massive, crinkly forms containing some fenestral fabric, and locally associated placers and small channels filled with eocrinoid debris suggest lower supratidal and intertidal conditions. Domal morphologies and interdome skeletal debris channels suggest lower intertidal to shallow subtidal, hypersaline to slightly hypersaline environments (Aitken, 1967; Playford and Cockbain, 1976). Thrombolite banks and mounds create a more patchlike configuration than the stromatolites. Both thrombolites and stromatolites are locally to pervasively dolomitized.

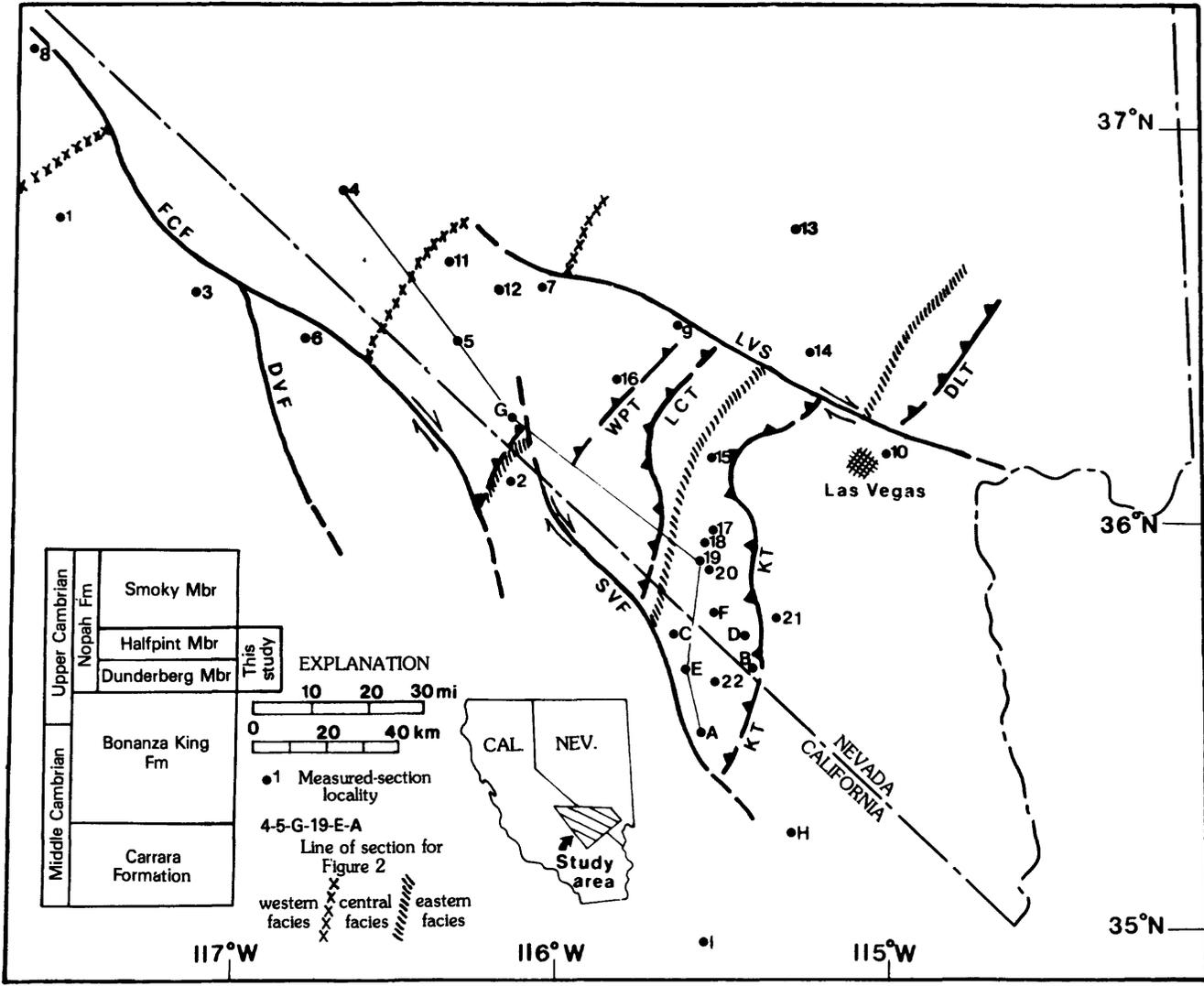


Figure 1.--Map of study area showing location of measured sections, major facies boundaries, and principal faults: FCF, Furnace Creek fault; DVF, Death Valley fault; SVF, Stewart Valley fault; LVS, Las Vegas shear zone; WPT, Wheeler Pass thrust fault; LCT, Lee Canyon thrust fault; KT, Keystone thrust fault; and DLT, Dry Lake thrust fault. Faults are dashed where approximately located. Measured sections: 1, Panamint Range; 2, Nopah Range; 3, Tucki Mountain; 4, Bare Mountain; 5, Ash Meadows; 6, Funeral Mountains; 7, Specter Range; 8, Last Chance Range; 9, Indian Ridge; 10, Frenchman Mountain; 11, Stripped Hills; 12, Specter Range; 13, Desert Range; 14, Fossil Ridge; 15, central Spring Mountains; 16-20, Spring Mountains; 21, Sheep Mountain; 22, Ivanpah Mountains; A, Mohawk Hill; B, State Line; C, Winters Pass; D, Devils Canyon; E, Mesquite Pass; F, Kirby Wash; G, Pahrump; H, New York Mountains, I, Providence Mountains.

**Lithofacies III.**--Individual beds and thick units of pelmatozoan packstone and wackestone in the Halfpint Member occur in the measured sections in the eastern part of the study area in close association with thrombolitic boundstone, and in places with stromatolitic boundstone. This lithofacies formed mainly in a belt between the stromatolite and thrombolite banks and in channels and ponds within the

algal complex. The stenohaline-normal marine eocrinoids (Sprinkle, 1976) that provided the abundant, highly fragmental skeletal debris, probably grew in gardenlike clusters immediately seaward of the algal bank system. Periodic storm waves raked across the eocrinoid meadows and swept the debris into interlacing channels between thrombolites. A significant volume of eocrinoid debris accumulated in

a shallow subtidal lagoonal basin leeward of the thrombolite complex (fig. 3).

**Lithofacies IV.**-- Medium to thick beds of oncolitic-skeletal packstone and wackestone in the Halfpint Member are confined to measured sections in the central part of the study area, and are in close association with thrombolitic boundstone. The oncolites are elliptical in shape and conform to the "C"-mode of Logan and others (1964). Stratigraphic relations suggest that the oncolitic sediments accumulated around the seaward margins of thrombolite banks and mounds in a subtidal environment of mild agitation. This interpretation is consistent with the views of Aitken (1967) and Gebelein (1976) on Cambrian cryptalgal carbonates in Alberta, Canada, and present-day oncolite formation in Florida Bay and the Bahamas, respectively.

**Lithofacies V.**--Oolitic wackestone, packstone, and grainstone units are confined stratigraphically to the Halfpint Member and geographically to the measured sections in the central part of the study area. Ooids are the dominant allochem in cross-stratified grainstone beds and lenses. Presumably, these deposits accumulated in a shoal belt of oolite sand bars, seaward of the algal bank system and in

wave-agitated shallow subtidal waters. The oolite shoal possibly developed along a break in slope separating shallow subtidal shelf from somewhat deeper inner subtidal shelf (Kepper, 1976). Closely associated oolitic skeletal wackestones and packstones probably represent storm washover-produced textural inversions in adjacent muddy bottom subtidal environments. Rare algal intraclasts and oncolites occur in the oolitic facies, but the separation of oolitic units and algal boundstones probably resulted because oolite bars and aprons provided shifting, unstable substrates not favorable for algal growth (Lohmann, 1976).

**Lithofacies VI.**--Dark, silty micrite containing few thin siltstone and calcarenite interbeds and some dark chert nodules composes the Halfpint in measured sections in the westernmost part of the study area; the micrite suggests deposition in outer shelf waters, well below normal wave base and generally below storm wave base. Sequences of lighter gray, thin, silty pelmicrite beds containing abundant silty seams and interlamination and thin- to medium-bedded bioclastic and intraclastic carbonates are characteristic of measured sections in the central part of the study area (figs. 1, 2). These lithologies suggest

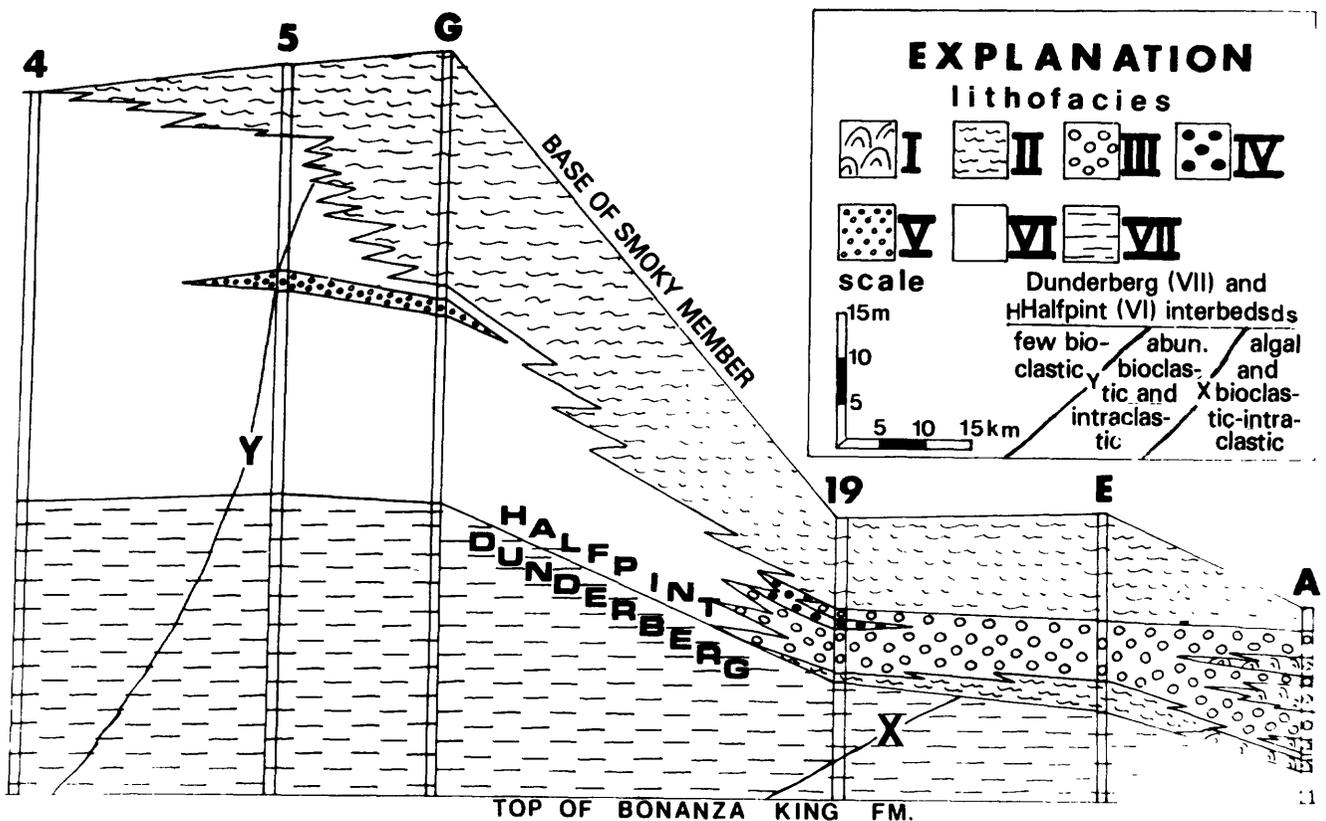


Figure 2.--Stratigraphic panel for line of measured sections (fig. 1) normal to depositional strike showing lithofacies and thickness relationships of Dunderberg and Halfpint Members.

deposition in a shallower, open-marine subtidal shelf setting, below normal wave base, but within the frequent influence of storm-wave base. The couplets composed of silty pelmicrite and interbedded skeletal or intraclastic units represent short cycles that reflect changing conditions (quiescent versus storm) within the open subtidal shelf setting. The production of such an abundant supply of large tabular intraclasts on the shelf perhaps can be attributed to the paucity of deep-burrowing infauna, a condition that allowed for extensive incipient cementation in the shallow substrate (Bambach and Sepkoski, 1979). Intraformational limestone breccias formed when subsequent storm waves stirred up the bottom and shredded the semilithified thin carbonate layers into slabs that were quickly redeposited. Essentially all of the intraclasts in lithofacies VI are silty pelmicrite, indicating derivation from the most predominant lithology in the Halfpint.

**Lithofacies VII.** - Terrigenous mud (Dunderberg Shale Member) accumulated in a spectrum of environments ranging from intertidal to deep outer subtidal. The relative abundance and kinds of carbonate interbeds within the Dunderberg (fig. 2) provide an index to the environmental setting. Shale sequences in westernmost sections (fig. 1) punctuated

by few carbonate interbeds (most of which are micrite) suggest deposition in moderately deep, outer shelf waters. Shale sequences in central measured sections (figs. 1, 2) containing thicker and more abundant interbeds of bioclastic hash and flat-pebble breccia suggest deposition in shallower, storm-influenced water. And finally, shale sequences in eastern measured sections (figs. 1, 2) containing thrombolitic and stromatolitic interbeds, as well as bioclastic and intraclastic beds having algal intraclasts, suggest shallow subtidal to intertidal environments. The shale in the Dunderberg is the textural analogue of the silty micrites and pelmicrites of the overlying Halfpint; as such the presence or absence of shale indicates relative availability of fine terrigenous material. Thus, the boundary between the succession of shale and carbonate half-cycles, expressed by the Dunderberg and Halfpint Members, respectively, does not reflect a major shift in environments, but rather the supply of fine terrigenous detritus. The main environmental shift occurred during later deposition of the Halfpint lithosome and is best observed in those central measured sections that show a stratigraphic cycle of lithofacies VI succeeded by interbedded lithofacies VI, IV, and V, and topped by lithofacies II (fig. 2).

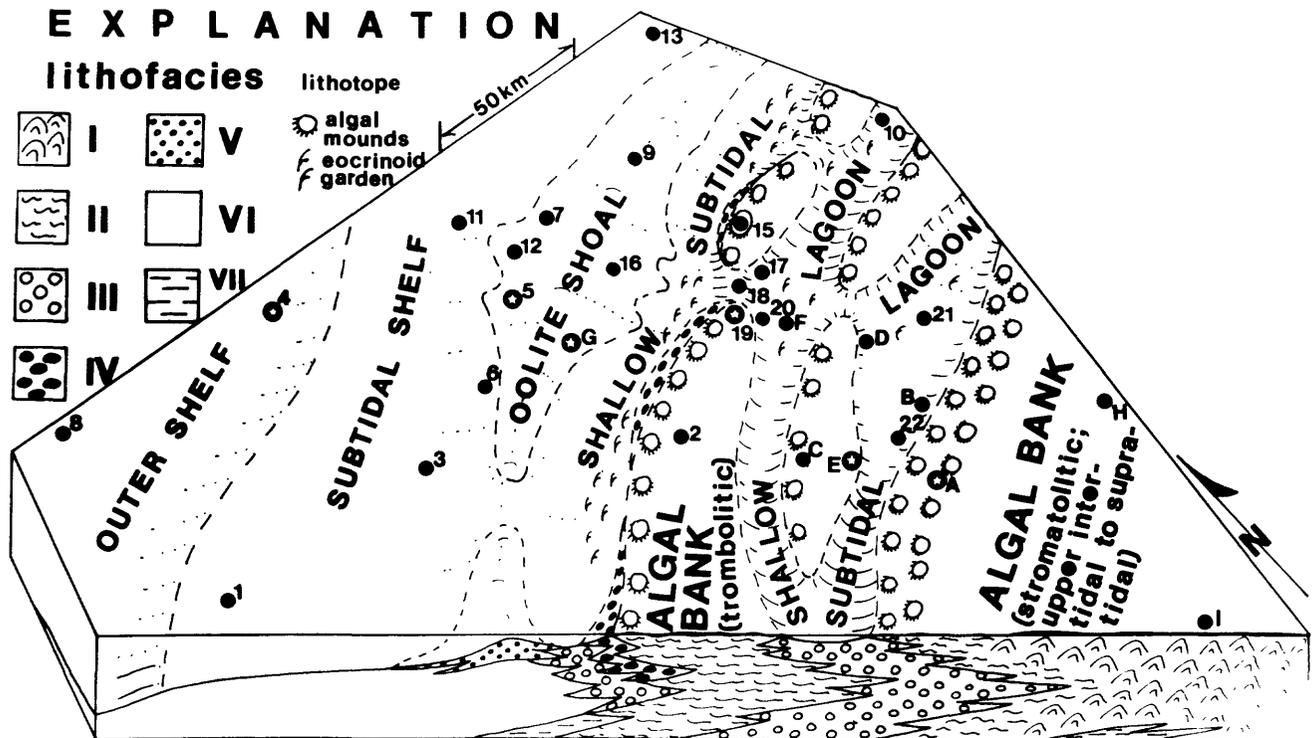


Figure 3.--Map and cross section showing interpreted paleoenvironmental patterns during deposition of upper part of Halfpint Member of Nopah Formation (*Elvinia* Biochron). Palinspastic restoration of sections to original relative positions utilizes base maps of Stewart and Poole (1974) and offset of major facies boundaries shown in figure 1. Measured-section localities (solid dots) are as listed in figure 1. Starred dots represent localities used to construct the cross section (fig. 2).

PALEOENVIRONMENTAL PATTERNS AND  
PALEOGEOGRAPHY

The study area lies astride the transition zone between the outer detrital and middle carbonate belts of Palmer (1971) and close to the hinge between the Late Cambrian craton margin and miogeoclinal shelf. During Dresbachian time, significant influx of offshore-derived fine terrigenous detritus accompanied a major transgressive phase, expressed by the migration of a shale lithosome (Dunderberg) over a peritidal carbonate lithosome (Bonanza King Formation). The terrigenous mud accumulated on a slowly subsiding, open-marine, storm-influenced subtidal shelf that supported trilobite-brachiopod communities (Miller and others, this volume). Dramatic thinning of sections from west to east occurred along a hinge line that trends between the eastern and central sections (figs. 1, 2). Terrigenous mud also accumulated on shallow subtidal bottoms and intertidal flats around and within a complex of thrombolite and stromatolite domes and mats making a patch reeflike configuration that represented the leading edge of a major algal bank system (fig. 3). More cratonward advance of the terrigenous lithosome was blocked by the massive algal carbonate buildup.

On a larger scale, during Dresbachian time, the district lay near the Equator in the doldrums belt (Scotese and others, 1979). Late Cambrian west-to-east wind patterns and ocean currents carried fine terrigenous material from exposed land areas, such as the Salmon River arch (Rowell and others, 1979), to the outer detrital belt.

Subsequent reduction of the terrigenous supply favored deposition of silty lime mud and pelletal lime mud on the open, storm-influenced subtidal shelf. Eocrinoid gardens flourished in normal-salinity, shallow subtidal environments along the frontal margin of the thrombolite patches and in a subtidal lagoon between the thrombolite- and stromatolite-dominated banks. Storms reduced the eocrinoids to carbonate skeletal sand that clogged intertidal and subtidal channels and larger subtidal ponds and small basins within the algal bank system (fig. 3).

A later regressive phase resulted in the seaward migration of the algal bank system and development of a marginal oncolitic belt and a more seaward oolitic-skeletal shoal-water to subtidal sand belt (fig. 3). The large-scale transgressive-regressive cycle probably was related to tectonic subsidence and perhaps also to eustatic sea-level changes. Smaller scale, generally coarsening upward stratigraphic cycles represent fair weather-storm cyclicity on the open subtidal shelf and a combination of storm and tidal cycle influences within the peritidal, algal-dominated complex. Continued seaward migration of the algal biosome through the remainder of the Late Cambrian produced

the massive carbonate (predominantly boundstone) lithosome that corresponds to the lower part of the Smoky Member of the Nopah Formation.

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## 17. ARCHAEOCYATHAN BUILDUPS: PIONEER REEFS OF THE PALEOZOIC

By

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The Archaeocyatha have long been recognized as important contributors to Early Cambrian carbonate sediments and were often collected from small separate carbonate buildups. However, prior to the 1970s, few Cambrian specialists recognized or appreciated their important pioneering role in the development of the complex biotic reefs which become abundant in the later Paleozoic. The last two decades of work in the Soviet Union, North Africa, and Europe, as presented two years ago in the Third Cnidarian Symposium in Warsaw, has outlined the main trends in the evolution of Lower Cambrian archaeocyathan buildups. New research from the Siberian Platform and western North America (R. A. Gangloff), Labrador and Newfoundland (N. P. James), and Sardinia (F. Debrenne) confirm and elaborate upon earlier findings.

The pioneering role of the Archaeocyatha and the general pattern of development in the Early Cambrian may now be summarized as follows:

1. The earliest buildups (bioherms) are found in the Lower Cambrian of the Siberian Platform. They are composed of a series of small, discrete mounds (calyptra of Soviet authors), which are usually less than 2 m in diameter and height. Archaeocyathan skeletal components are commonly accessory elements, with algae being dominant components of bioherms.
2. In the Atdabanian Stage, individual bioherms are larger, and many of them coalesce to form extensive buildups which are topographically and geographically significant. Algae such as Renalcis and Epiphyton are dominant, and archaeocyathans either are scattered irregularly throughout the structures or,

more commonly, are found in nodular masses within perireefal sediments. The relative proportion of archaeocyathans within the buildups is significant, over 20 percent. In upper Atdabanian strata, the Archaeocyatha have become colonial and show a greater variety of morphologic types.

3. During the late Atdabanian and Lenian Stages, and especially in the Elankian Stages, just prior to extinction of the Archaeocyatha, bioherms with as much as 50 percent archaeocyathan skeletons were common. The combination of prolific skeletal carbonate production, the great variety of shapes, and the abundance of colonial types created topographically prominent buildups and an increase in the diversity of ecologic niches. The new niches were filled by a great variety of skeletal and sediment-producing organisms. At this stage of development, archaeocyathan-rich buildups represent a biotic and structural prototype for reef development later in the Paleozoic. Archaeocyathans, when found in the more complex buildups or reefs, consistently exhibit budding, dissepimentation, and (or) exothecal outgrowths. These coenosteum-like exostructures often bind exceptionally large and highly polymorphic archaeocyathans together. In addition to abundant algae, these early reefs commonly include a great variety of associated organisms, including forms that may represent symbionts, borers, and herbivorous grazers.

## 18. MICROSTRUCTURE OF TABULAONUS AND ITS SIGNIFICANCE TO THE TAXONOMY OF EARLY PHANEROZOIC ORGANISMS

By

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The last two decades have seen considerable increase in the number of described taxa of Cambrian fossils with calcareous skeletons. The zoological affinities for many of these forms remain obscure or uncertain, and most attempts at delineating relationships have approached the problem through comparative anatomy of gross structures. We propose to approach the question by means of microstructural studies of the skeleton. The abundance of relatively well preserved specimens of Tabulaonus Handfield from a locality on the Tatonduk River in central-east Alaska has allowed us to do this. Two techniques have been used. Ultra-thin polished sections were studied with the aid of a high-power light microscope and a standard scanning electron microscope.

The central question in all paleobiologic investigations into microstructure is whether the observed morphologies are taxonomically valid, since they most certainly have been modified by diagenetic processes. In the case of Lower Cambrian fossils, they may have been modified by several episodes of diagenesis and (or) metamorphism. The comparison of several kinds of fossils (three Archaeocyatha, Epiphyton, and Renalis) found associated with Tabulaonus was chosen as a method of approaching this question. It is assumed that all of the skeletal remains of these taxa have been subjected to nearly the same diagenetic processes. Therefore, any significant observable differences in the microstructure between taxa should reflect original differences which maybe taxonomically useful. The results of this investigation into the enigmatic form Tabulaonus demonstrate that it possesses a microstructure that is fundamentally different from that of all other taxa associated with it in the same thin sections.

Tabulaonus has a wall that consists of discontinuous concentric layers of alternating dark and light zones. The dark zones are slightly embossed granules (average diameter 3 micro-m). The light zones consist of irregular elements, sometimes elongated and always larger than the dark units (7-20 micro-m). Where elongate, they are arranged perpendicular to the surface of the wall. The three forms of Archaeocyatha--Yukonocyathus Handfield, Cordilleracyathus Handfield, and Acanthopyrgus

Handfield--possess very similar microstructural patterns consisting of polyhedral units (6-12 micro-m in diameter). Each polyhedral unit is embossed and yields a puzzlelike design in section. The algae, that are present in the same sections, Renalcis and Epiphyton, are composed of equidimensional or elongate granules with smooth surfaces and range from 3 to 5 micro-m in diameter. The microstructure of Tabulaonus, as discerned in this study, eliminates consideration of this taxon as an archaeocyathan or as an algae such as Epiphyton or Renalcis.

The presence of a colonial form, rudimentary septa, and a tabularium remove Tabulaonus from the Gastroconidae Korde, to which they had been assigned by Handfield. The presence of at least two different types of microstructural units suggests a more elaborate process of primitive algae. The microstructure is not characterized by the "fibers" of primitive or advanced corals. A comparison with the primitive Cambrian coral Cothonion reveals that Tabulaonus has not yet reached this grade of microstructural evolution. However, the microstructure of Tabulaonus, in combination with its coralline-like gross morphology, best supports an assignment to the Zoantharia.

During the course of this investigation it was recognized that Bacatocyathus Vologdin is most probably an example of Tabulaonus rather than an archeocyathan. Bacatocyathus has been reported from a number of areas within the U.S.S.R. Specimens of this taxon have not been obtained by us for careful comparison. However, additional studies may show that the stratigraphic and geographic range of Tabulaonus is extensive. In addition, if these two genera are the same, it would be possible to trace the earliest differentiation of the Zoantharia back to the Tommotian Stage.

## 19. ARCHAEOCYATH OCCURRENCES AND TECTONIC MOVEMENTS IN THE CANADIAN CORDILLERA

By

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New localities of archaeocyaths have been found on both sides of the Rocky Mountain trench between 56°N. and 60°N. (fig. 1). West of the trench, archaeocyaths are usually in two carbonate members (50-100 m each), and they do not appear in the intervening silty member. Many of the archaeocyaths are associated with algal structures, oolites, and oncolithes. On the east side of the trench archaeocyaths are found in lenses of carbonate, possibly bioconstructed, interbedded in siltstone and sandstone (J. L. Mansy, 1975, 1976). The contrast of lithofacies and fossil associations and the abrupt thickness change between the two sides of the Rocky Mountain trench, are attributed to a 400-km right-lateral displacement along the Tintina-Rocky Mountain trench fault (Tempelman-Kluit, 1979; Mansy, 1981).

The western fauna is dominated by Irregulares: abundant Archaeocyathus borealis Okulitch occurs with ?Metaldetes caribouensis Handfield, different morphotypes of Flindersicyathidae, less numerous Clarucoscinus obliquus (Okulitch), ?Metacoscinus gabrielsensis (Okulitch), Archaeocyathus atlanticus Billings, and scattered Regulares, belonging to the Ethmophyllidae, Diplocyathellidae, and Robustocyathidae. The archaeocyaths, despite the presence of some well developed exostructures, are not sufficiently massive to build true reefs. Many of them occur as bioclasts together with hyolithids, hyolithelloids, trilobite fragments, echinoderm plates, and rare Chancelloria. Small clusters of algae (Renalcis) are present.

Within the eastern fauna, Irregulares are not only less abundant than Regulares, but also less diversified than on the west side of the Trench. In both groups, the species are represented by stacked small cups (average diameter 5 mm) many of them bounded by algal structures (Renalcis and scarce Epiphyton). Bioconstructions might be considered here.

Handfield's (1971) description of species of Sekwicyathus, Yukonocyathus, Cordilleracyathus, Acanthopyrgus, Tabulaconus (a possible coelenterate) in collections he made from localities on the east side

(62° N.-64° N.) strengthens the idea that the difference observed in the faunal assemblages on the two sides of the trench has to be considered not only in terms of biostratigraphic changes or ecological variations, but also in connection with the lateral displacement along the Tintina-Rocky Mountain trench fault.

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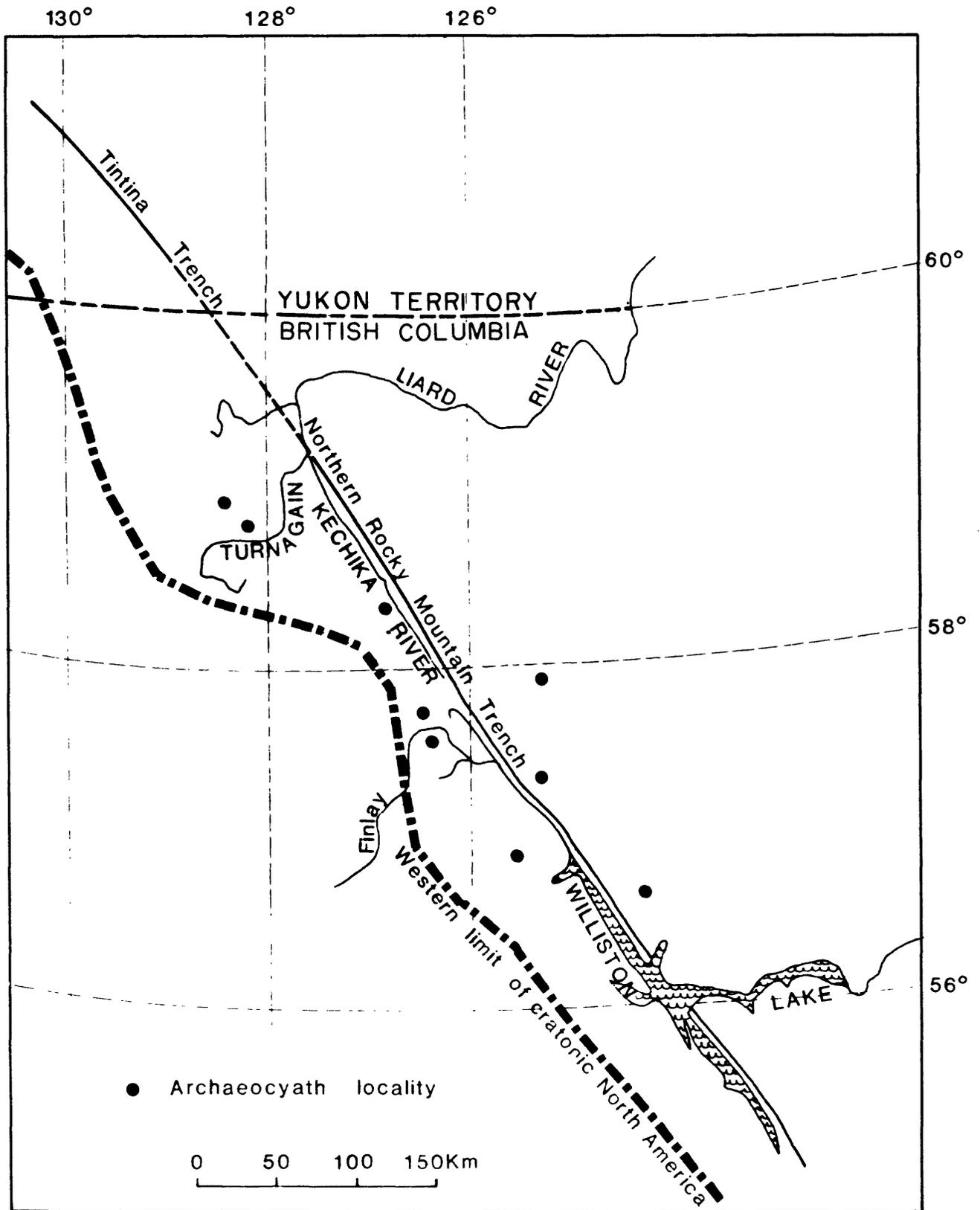


Figure 1.--Location of Tintina-Rocky Mountain trench fault and archaeocyath localities in western Canada.

## 20. PATTERNS OF PLATFORM AND OFF-PLATFORM CARBONATE SEDIMENTATION IN THE UPPER CAMBRIAN OF THE CENTRAL APPALACHIANS AND THEIR IMPLICATIONS FOR SEA LEVEL HISTORY

By

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The Lower Cambrian to Middle Ordovician Great American Bank of the Appalachians is an eastward-thickening wedge of shallow peritidal platform carbonates 3000 km long, at least 150 km wide, and more than 3000 m thick. In the central Appalachians (West Virginia, Maryland, and Pennsylvania), during the Cambrian, deeper water off-platform carbonates accumulated to the east of the bank but by the Early Ordovician this basin had shallowed to near sea level as the platform prograded eastwards.

Despite the history of folding and faulting of these rocks, quite detailed reconstructions of depositional environments are made possible by the excellent preservation of primary sedimentary structures and textures. To illustrate the kinds of depositional features preserved, the mode of organization into environmentally significant facies, and the distribution of patterns of these facies, we focus on the Upper Cambrian of Maryland. Here, the platform facies are represented by the Conococheague Limestone (750 m thick) of the Great Valley, whereas the off-platform facies are contained in the Frederick Limestone (800 m thick) of the Frederick Valley.

### PLATFORM CARBONATES OF THE CONOCOCHEAQUE LIMESTONE

The basic lithostratigraphic units in the Conococheague are subfacies, packages of rock 0.01-2.0 m thick with distinctive sets of internal sedimentary structures, textures, and other syndepositional features diagnostic of specific depositional subenvironments. The subfacies are grouped into facies, each of which is equated with a specific depositional environment. We have recognized three main facies: (1) tidal-flat facies, (2) shelf-lagoon facies, and (3) shelf-margin facies.

#### Tidal-Flat Facies

Ribbon-rock subfacies.--Ribbonrocks are intimately interbedded thin limestone and dolostone beds. Typically, the limestones are (1) peloidal fine sands in centimeter-scale ripple-form wavy beds, and

(2) lenses of flat and edgewise intraclast conglomerates. The rippled peloidal sand beds are internally wave-and-current-ripple crosslaminated. The interbedded lutitic dolostone beds are continuous and have mudcracks, and drape the rippled tops of underlying limestone beds. In some places the overlying limestone beds penetrate the dolostone beds as load casts. The observations suggest that the limestone-dolostone interbeds of ribbonrocks reflect original sand-mud alternations, strikingly similar to interbedded siliciclastic sands and muds (wavy bedding) of the modern macrotidal North Sea intertidal flats (Demicco, 1980), which we believe to be the likely depositional analog.

Wavy prism-cracked laminite subfacies.--This subfacies is a laminated version of the ribbon-rock subfacies with which it is gradational. Small LLH stromatolites and jelly-roll structures are common. Deep (as much as 1 m) prismcracks and rare sparry calcite nodules (a few containing gypsum) disrupt this subfacies. A regularly desiccated, high intertidal mudflat coated with a sediment-trapping mat similar to the intertidal algal mudflats of the Persian Gulf, is the inferred depositional setting. Interpretation of the nodules as intrasediment evaporite-mineral growth points to a semiarid or arid climate.

#### Shelf-Lagoon Facies

Ribbon-rock subfacies.--This subfacies is made up of ribbonrocks identical to those of the tidal-flat facies except that the dolostone interbeds do not have mudcracks. This implies a subaqueous depositional setting for these rocks. Analogous subtidal wavy bedding is common in a number of modern macrotidal estuarine and shallow shelf settings.

Cross-stratified grainstone subfacies.--Sets of calcite grainstones 5-10 cm thick occur in cosets 0.5 to 2.0 m thick. These rocks are composed of various admixtures of sand-size ooids, peloids, skeletal grains, and quartz grains. The sets are both tabular-planar and hummocky cross-stratified. A few massive beds are disrupted by millimeter-scale tubes filled with dolomitic mud. Hardgrounds, surfaces with submillimeter micritic rinds, along which detrital

grains have been truncated, are found in these rocks. This subfacies is interpreted as having been deposited in ooid-peloid shoals, generally active but occasionally inactive for long enough periods to allow penecontemporaneous cementation and burrowing to occur. The shoals were composed of sand waves and wave swash bars similar to ooid-peloid sand blankets and shoals of the Bahama Banks and outer south Florida shelf.

Flat-pebble conglomerate subfacies.--Flat-pebble conglomerates occur in widespread sheets 10-50 cm thick. The clast size of these deposits ranges from tens of centimeters to the sand sizes. Internally, these beds have a crude horizontal fabric. The conglomerates are polymict; however, the major clast type is hummocky, cross-stratified ooid-peloid grainstones. Internally, these sand clasts have a noncompacted textural packing and an outer sub-millimeter micritic rind along which grains are truncated. The obvious source of this clast type is the early cemented sands of the grainstone subfacies. The sheet-like nature of these beds, the large clast size, and the range of sizes suggests that these are storm lag gravels.

Thrombolite subfacies.--Cryptalgal mounds (thrombolites) from tens of centimeters to tens of meters across, surrounded by other shelf lagoon subfacies, are common in the Conococheague. Internally, their clotted fabric consists of an upward-directed anastomosing network of centimeter-scale micritic fingers that contain patches of Girvanella and Renalcis and are encrusted with Renalcis or a micrite rind. Interfinger areas are filled with a skeletal packstone in which the remains of an abundant diverse marine fauna is preserved. The fingers and interfinger areas are cut by cavities lined by Renalcis or a micritic rind and filled geopetally with internal sediment and sparry calcite. The presence of framework building and encrusting organisms, dissolution and internal sedimentation, and an abundant invertebrate fauna suggests that these bioherms are analogous to modern coralgal patch reefs, such as on the south Florida shelf.

Graded, thin-bedded dolostone subfacies.--These beds are 2-8 cm thick. The base of each bed is usually a fine to medium sand, rich in quartz and dolomitic peloids, that commonly has an internal undulatory lamination. This sand base grades upward to a dolomitic mud, which in some places has a grumulous structure suggestive of an original peloidal texture. These deposits are probably the result of the fallout and reworking of detrital sediments from a decelerating pulslike flow. Storm-reworked intershoal and interpatch reef areas are the interpreted site of deposition of this subfacies.

## Shelf-Margin Facies

In the central Appalachians, the platform carbonates exposed in the Great Valley are separated from the off-platform carbonates of the Frederick Valley by the South Mountain anticlinorium, so that the Late Cambrian platform margin is not preserved. However, the margin facies can be reconstructed from presumed allochthonous blocks in the breccia subfacies of the off-platform facies.

EPIPHYTON framestone subfacies.--This subfacies consists of framestone mainly built by bushy colonies of Epiphyton and small submillimeter platy crusts, cemented by sparry calcite. This fabric is crosscut by large vugs lined with a radial cement having a geopetal internal dolomitic sediment and sparry final void-filling cement. This is the same fabric reported by Pfeil and Read (1980), who interpreted such framestones as shelf-margin Epiphyton reefs.

Ooid-peloid grainstone subfacies.--This subfacies consists of sand-size intraclasts, ooids, and peloids. These grain types are most commonly the products of shallow shelf environments. We presume that this material was derived from the shelf margin where it was perhaps found in interreef shoal areas.

## Facies Patterns

Shelf-lagoon facies dominate the vertical column from bottom to top, but there are two separate, well-defined zones (one 30 m and the other 50 m thick) where tidal-flat facies interrupt this pattern. There are no progressive vertical trends within the platform facies that can be interpreted as megacycles. However, there are second-order changes in the shelf-lagoon facies on the subfacies level. For example, packages of shelf-lagoon facies tens of meters thick may be dominated alternately by large thrombolites or ribbonrocks, or cross-stratified grainstones. In the tidal-flat facies zones, shallow shelf-lagoon and tidal-flat subfacies are organized into well-developed fining-upwards cycles: flat-pebble conglomerate/cross-stratified grainstones to thrombolites to ribbonrocks to wavy prism-cracked laminites. These cycles are as much as 10 m thick, have sharp basal and upper contacts but internally gradational boundaries, and record increased shoaling and exposure upwards. These cycles are thought to represent the progradation of tidal-flat facies over shallow subtidal shelf-lagoon subfacies. Laterally, the cyclic zones can be traced tens of kilometers from the west to the eastern limit of outcrop, and individual cycles can be traced over approximately 200 km<sup>2</sup>.

Within the shelf-lagoon facies, individual subfacies can also be traced across the area, making mappable lithostratigraphic units. The overall effect is a local layer-cake stratigraphy.

## OFF-PLATFORM CARBONATES OF THE FREDERICK LIMESTONE

The Frederick Limestone has been studied in detail by Reinhardt (1977). In contrast to the platform carbonates of the Conococheague, the off-platform carbonates of the Frederick are poorly exposed and do not have well-known modern analogs. Although we agree with a basinal setting for these rocks, we believe the exact geometry of the slope-basin transition is not at all clear.

### Off-Platform Facies

Breccia subfacies.--Thick beds (as much as 5 m) of polymict breccias are found in the Frederick Limestone. Blocks are as large as meters in size. Most of the clasts are of the thin-bedded limestone subfacies, but a significant percentage are blocks of shelf-margin sands and Epiphyton framestones, the geopetal void infills of which unequivocally show transport rather than in situ growth. Clearly, these thick breccias represent a slope deposit of some type, but the exact nature is uncertain.

Thick-bedded peloidal grainstone subfacies.--These meter-scale beds of grainstones contain coarse, rounded intraclasts, quartz grains, ooids, and skeletal grains. The composition of the grains suggests, that they were derived from the shelf margin of the shelf itself.

Thin-bedded, graded limestones.--The bulk of the Frederick is a monotonous repetition of 2-8 cm thick beds, separated by millimeter-scale shaly partings. Internally, the thin beds are usually graded and show a host of current features including: small-scale scour and fill, parallel flat and undulatory laminations, ripple cross lamination, and rarely Bouma sequences. These beds show a systematic variability in their fossil content and degree of bioturbation (see below). These beds were probably deposited from pulslike waning downslope currents, perhaps generated by storms.

### Facies Patterns

Unlike the platform deposits of the Conococheague, the 800 m of the Frederick has a recognizable vertical pattern (a megacycle). Although the entire package is overwhelmingly dominated by the thin-bedded limestone subfacies, the basal one-third of the Frederick is characterized by the presence of the breccia and peloidal grainstone subfacies. These two

subfacies decrease in thickness and abundance through the middle third of the Frederick and are absent from the upper third. Complementing this decrease in thickly bedded units is an upward increase in fossil content and bioturbation of the thin-bedded limestone subfacies in the upper third of the formation. The Upper Cambrian Frederick is conformably overlain by Lower Ordovician peritidal platform carbonates of the Grove Limestone. These changes are interpreted as representing the shallowing of a periplatform apron of carbonate sediment prior to the eastward progradation of the platform.

## CONCLUSIONS

For roughly 100 m.y., the Central Appalachians was the site of platform carbonate sedimentation in water depths perhaps never greater than 10-20 m. During the Late Cambrian, at least, the platform was dominated by a high tidal range, rough water, and a dry climatic setting.

Tectonic stability during building of the platform is implied by the estimated net relative subsidence rate of no more than 6 cm/1,000 years, two to three orders of magnitude less than Recent isostatic crustal readjustments in Fennoscandia.

Off-platform carbonates do not record an adjacent deep oceanic basin. In fact, by the latest Late Cambrian-Early Ordovician, these off-platform carbonates had been overrun by the eastward progradation of the platform. The gradual upward shoaling of these off-platform carbonates and the paucity of slope breccias suggest that the Cambrian-Ordovician platform-to-basin transition was a ramp rather than a buttress (see Reinhardt, 1977; Pfeil and Read, 1980).

In the platform carbonates, time lines must be contained with the shelf lagoon-tidal flat cycles because the cycles are traceable across the area. So lithostratigraphic units are almost chronostratigraphic markers. Therefore, the layer-cake platform sequence must record many small-scale relative sea-level changes. Large-scale sea-level trends such as the massive sea-level rise postulated for the Cambrian (Vail and others, 1977, fig. 1) are not recorded on the platform carbonates. Indeed, even the large shoaling cycle of the off-platform carbonates is not reflected in the coeval platform sequence. We conclude, therefore, that massive accumulations of stable platform carbonates are not good prospects for identifying major global sea-level changes. The reason for this lack of relationship may be because carbonate platforms are efficient sediment-producing factories that can respond rapidly to subsidence and so maintain depth close to sea level for millions of years.

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## 21. MORPHOLOGICAL DIVERSITY OF EARLY CAMBRIAN ECHINODERMS

By

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Echinoderm specialists have described a number of Cambrian and Ordovician classes and subphyla (Sprinkle, 1980). These higher taxa apparently stopped differentiating after the Ordovician, while lower taxa continued to diversify. Theoreticians (for example, Valentine, 1980) have begun to explain this pattern, their faith buoyed by reports of similar diversity patterns for the mollusks (Yochelson, 1979), arthropods (Whittington, 1979), and problematica (Conway Morris, 1979).

Potential explanations for this taxonomic diversity pattern include four hypotheses:

Hypothesis 1: Taxonomic hindsight.--Taxa based on Holocene specimens may lose their distinctiveness among earlier, less divergent species. Figuratively, today's class may be yesterday's order and last year's family. By recognizing Cambrian families as classes, we may be forcing ourselves to recognize many additional taxa at equally high rank.

Hypothesis 2: Taxonomic inflation.--The notion of large numbers of early Paleozoic classes is popular. Perhaps exuberant taxonomists are filling the demand by elevating the rank of their unusual Paleozoic taxa.

Hypothesis 3: Missing fossil record.--Cambrian classes may have begun their differentiation hundreds of millions of years before the Cambrian, but our fossil record is biased against Precambrian organisms (Durham, 1978).

Hypothesis 4: Higher taxa evolve most rapidly at the beginning of their history.--Evolution may work differently at the beginning of a phylum's history. Perhaps the modern biosphere selects against large morphological jumps, whereas such changes occasionally survived in the early Paleozoic (Valentine, 1980).

An element of truth may be found in each of these hypotheses.

In this report, I argue that Early Cambrian echinoderms belong to only two major groups and that at least part of the phylum's differentiation into subphyla and classes happened after the Precambrian. In the arguments that follow, some taxonomic problems of hypotheses 1 and 2 are dismissed by looking at "phylogenetically unconnected groups" instead of classes or subphyla. This approach is

unavoidably subjective, but it allows me to present a list of the largest morphological discontinuities within the phylum. These discontinuities separate major clades, and the earliest member of each clade marks the latest time that each could have differentiated.

Hypothesis 3, which assumes a long Precambrian history for the phyla, can be eliminated by finding Phanerozoic morphologies that are intermediate between major clades. Failing this, the hypothesis can be compromised by showing that few "unconnected groups" occur in the earliest part of the fossil record and that most unconnected groups appear significantly later. If some groups are shown to have evolved after the beginning of the Cambrian, there is less need to hypothesize long periods of Precambrian history for the remaining groups. The strongest argument in favor of hypothesis 3 points to the large morphological gaps between early taxa and says that there is simply too much of a gap for 30-40 million years of evolution to be responsible. In effect, if I can show that evolution has produced several gaps in a few tens of millions of years, then the strongest argument in favor of hypothesis 3 becomes inappropriate.

Hypothesis 4 can be eliminated by finding morphologically primitive Precambrian echinoderms; the older these fossils are, the more justified would be the rejection. However, Ediacaran faunas, Precambrian acritarchs, and Vendian shelly fossils show that appropriate marine facies are available, so the lack of Precambrian echinoderm fossils suggests that none will be found.

Microporous, monocrystalline calcite plates are probably uniquely derived characters, as argued by Ubachs (1975) and Jefferies (1979). I accept these arguments and assume that the phylum Echinodermata is monophyletic. Hypotheses 3 and 4 predict different amounts of elapsed time between the derivation of this phylum-level skeletal character and the beginning of the echinoderm fossil record. Since I place my discussion between these two events and analyze the latter, it is not appropriate to use a character that was derived at the earlier time. For this reason, I do not use skeletal composition or microstructure as characters for linking my "unconnected groups."

## DESCRIPTIONS

**Edrioasteroids.**--An edrioasteroid is a plated echinoderm that has five ambulacral food grooves which meet at a centrally located dorsal mouth and that lacks appendages. The food grooves are limited to the dorsal surface and they are arranged in a 2-1-2 pattern (see Sprinkle, 1973). In addition, a rosette-like anal pyramid and a small third aperture are always located in the same interambulacrum, opposite the unbranched food groove.

**Camptostroma roddyi** Ruedemann (figure 1) is a large edrioasteroid found in the Lower Cambrian Kinzers Formation of southeastern Pennsylvania. The dorsal side of the body is covered by small epispire-bearing plates. On the ventral side, the plates are imbricate and tightly sutured. Proximally, the ambulacral plates are small and difficult to distinguish from epispire-bearing plates. The distal ambulacrum is composed of larger plates. Both ambulacral plates and the cover-plate sheets have a series of secondary grooves perpendicular to the main food groove. Each secondary groove is carried on one or two rows of cover-platelets. These rows of platelets join together, forming the coverplate sheet.

**C. roddyi** lacks a heavy oral ring, a character that is found in virtually all later edrioasteroids. This, lack and the presence of an ambulacrum constructed of simple plates, wide coverplate sheets, dorsal epispires, and lengthy proximal food grooves are judged to be primitive features within the edrioasteroids and found in **Camptostroma**.

A small, undescribed edrioasteroid occurs with **C. roddyi**. It is distinct from the equal-sized young **Camptostroma** in that it has imbricate dorsal plates, nonimbricate ventral plates, a peripheral rim composed of "geniculate plates" (after Bell, 1976), and a distinctly different type of coverplate. The ambulacral plates are small and flat, and they have small or nonexistent ambulacral pores. The cover-plates themselves are slender, and many are crowded onto each ambulacral plate. I do not know if this species possessed an oral ring.

Other Early Cambrian edrioasteroids include **Stromatocystites walcotti** Schuchert and an undescribed species from California (Durham, 1967; Sprinkle, 1973: pl. 25, figs. 13, 16, 17). Both forms are poorly known, but they fall within the range of edrioasteroid morphologies described from younger rocks.

**Blastozoans.**--Blastozoans are echinoderms with unbranched feeding appendages called brachioles. Primitive blastozoans are constructed like a camptostromatoid or stromatocystoid edrioasteroid, with the addition of brachioles mounted along the sides of each food groove. The oldest known blastozoans are Early Cambrian lepidocystoids from the same rocks that contain **Camptostroma roddyi** (figure 1) and

ecocystitid eocrinoids from Pennsylvania and California. Although blastozoans reached a modest diversity by the end of the Cambrian, their major morphological and taxonomic diversification occurred during the Ordovician (Broadhead, 1980).

The lepidocystoid food groove has the brachioles attached to ambulacral plates, between the ambulacral pores. These separated brachioles and ambulacral pores suggest that a water vascular system did not extend into the brachioles (see Sprinkle, 1973). Some type of water vascular system existed in advanced blastozoans, such as **Jaekelocystis hartleyi** (see Kesling, 1961), so intermediates like the ecocystitid eocrinoids probably had a water vascular system too, although middle Middle Cambrian species (for example, **Gogia longidactylis** Walcott) lack ambulacral pores. Possibly, ambulacral pores (and the ambulacral tubefeet which pores imply) are edrioasteroid-derived characters that were inherited by the earliest blastozoans and lost soon afterward.

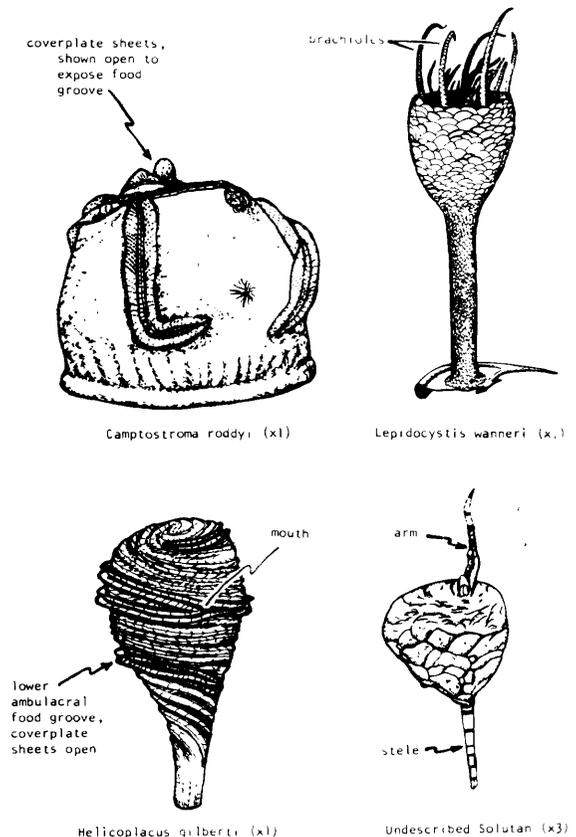


Figure 1.--Reconstructions of four Early Cambrian Echinoderms.

**Helicoplacoids.**--Helicoplacoids have become a textbook example of Early Cambrian evolutionary experimentation (for example, Dott and Batten, 1976, p. 190). The fossils are found in the western Great Basin and eastern British Columbia. My interpretation of these fossils, presented below, is different from the

original model of Durham and Caster (1963). It is based upon a detailed restudy of the types and many additional specimens.

Helicoplacoids have three ambulacral food grooves. Two food grooves spiral upward from the mouth, which is located on the side of the body, while the third spirals downward (fig. 1). All three ambulacra were lengthened during ontogeny by the addition of new plates at their distal tip, in the manner common among echinoderms. The anus is not identified with certainty, but may have been situated at the animal's upper pole. An elongate holdfast elevated the animal above the substrate.

The ambulacral plates, ambulacral pores, coverplate sheets, and the grooves on the inner surface of the coverplates are similar to those found on early edrioasteroids. I find no evidence of compound ambulacral plates or a mouth frame.

Solutan carpoids.--Solutan carpoids have a globular, asymmetrical body that is usually flattened. A single, unbranched feeding arm extends from the mouth, and another unbranched appendage called the stele extends from the opposite end of the body. The anus is along the side of the body, midway between the arm and the stele. A third aperture occurs on the body near the mouth.

The earliest known solutan is an undescribed species from Pennsylvania (Derstler, 1975). The animal is weakly plated, except for the arm and stele (fig. 1).

Other Echinoderm Groups.--Ubaghs (1967) and Sprinkle (1973) have pointed out that Cymbionites craticula Whitehouse and Peridionites navicula Whitehouse are unclassified echinoderm scraps. These fossil fragments provide no justification for the taxonomic and implied evolutionary significance they have been given (Hyman, 1955).

Several undescribed Early Cambrian echinoderms have food grooves mounted on top of the dorsal, epispire-bearing plates. Sprinkle (1973, pl. 25, figs. 20-22) illustrates isolated plates of one species. Another species, from Pennsylvania, appears to have normal edrioasteroid ambulacra that extend distally onto the dorsal plate surface. One scrap of a third species, from Inyo County, Calif., has a twice-branched food groove. These forms appear related to edrioasteroids.

The earliest known echinoderms are disarticulated plates from the middle Lena Stage carbonates of the Siberian Platform (A. Yu. Rosanov, personal communication, 1976) and equivalent-age plates from California (Durham, 1967). I have not seen the Siberian specimens, but the California fossils include small (1-2 mm), rectangular and polygonal plates and larger (4-6 mm), thin, epispire-bearing plates. While I have not been able to determine their class-level affinities, these fossils are easily accommodated within described Early Cambrian groups.

## DISCUSSION

Lepidocystoid eocrinoids and camptostromatoid edrioasteroids have similar body plans, with the obvious difference of the lepidocystoid brachioles. The brachioles do not appear to have water vascular connection (see above), and I can find no fundamental difference between lepidocystoid brachioles and the camptostromatoid coverplate sheet. Both consist of one or two rows of platelets, which are attached to an ambulacral plate. Both have a secondary groove facing the main food groove; the secondary grooves are lengthened by the addition of new platelets distally and, in both, new secondary grooves are added at the distal end of the main food groove. No major morphological or morphogenetic shift is required to derive brachioles from edrioasteroid coverplate sheets. Because I cannot find substantial differences between early edrioasteroids and blastozoans, I believe that the two are closely related and that they form a phylogenetically connected group.

Adult helicoplacoids and edrioasteroids share the same type of ambulacral food groove and coverplate sheet. Cambrian echinoderms display at least five other feeding structures besides the edrioasteroid-helicoplacoid type. These include the solutan arm, stylophoran aulacophore, cinctate food grooves, ctenocystoid structure, and crinoid arms. There is, at most, one chance in five that the edrioasteroid feeding structure represents the primitive feeding condition. Taking these odds at face value, the edrioasteroid food groove is probably derived. If true, then helicoplacoids join edrioasteroids and blastozoans to form a single clade. This hypothesis could be disproved by finding serious inaccuracies in my interpretation of the fossils or by showing that the edrioasteroid-helicoplacoid-blastozoan ambulacrum is not uniquely derived.

Solutan carpoids and the edrioasteroid clade share only the basic echinoderm skeleton: a separate mouth and anus and a third aperture. These are phylum-level characters, which are useless for distinguishing finer scale phylogenetic ties. I can find no morphological connections between solutans and edrioasteroids. For this reason, I consider solutans to be a second, phylogenetically unconnected clade.

Three to five unconnected groups appear in Middle Cambrian rocks. These include stylophorans, cinctate carpoids, ctenocystoids, cyclocystoids (if they are not related to the edrioasteroids), and one questionable crinoid. (Crinoids definitely occur in the uppermost Cambrian, as evidenced by an unstudied hydrocrinoid-like form from Montana.) Two more unconnected groups appear in Ordovician rocks, including the asteroids and the echinoid group. The first occurrence of each group is plotted in figure 2A.

It is instructive to compare these data (figure 2A) with the results of a simple diversity experiment, presented in figures 2B and 2C. The experiment began

with a set of 30 "species," all with identical ranges and equal abundance. The species were arbitrarily divided into eight "unconnected groups," which contained from one to nine species (9, 1, 2, 5, 4, 2, 3, 4). This species matrix was randomly sampled ( $p_{\text{survival}}=0.05$ ) to simulate the fossil record. Despite the simultaneous appearance of thirty species in the unsampled record, the sample shows a gradual rise in apparent diversity (fig. 2C). First appearances of the unconnected groups form a single peak on the histogram in figure 2B.

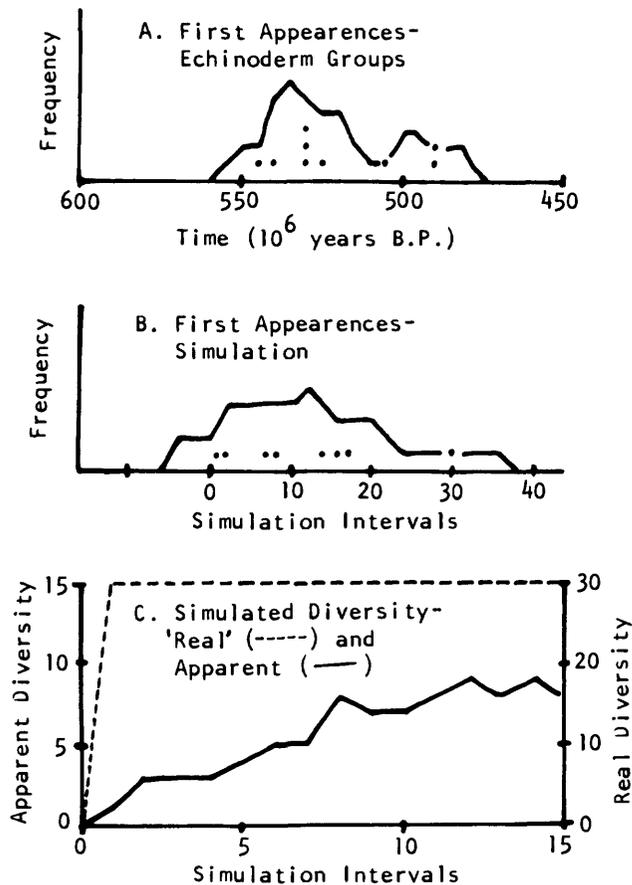


Figure 2.--First appearances and diversity patterns of Early Cambrian echinoderms. A, First appearances of phylogenetically "unconnected" echinoderm groups. Histogram smoothed with 30-m.y. running average. B, First appearances of simulated clades. Histogram smoothed with 12-interval running average. C, Comparison of "real" (assumed) and apparent (sampled) diversity from simulation.

Two points are brought out by this simulation. First, sampling effects have probably made the Precambrian-Cambrian diversity rise appear much smoother and more gradual than it really was. Second, sampling effects are probably not responsible for the two peaks on figure 2A. Unless the Cambrian groups were relatively diverse and common, while the "Ordovician" ones were consistently rare and nondiverse throughout the Cambrian, sampling could not produce a two-peaked histogram of first occurrences. Barring this possibility, at least some of the groups with Ordovician first appearances must have evolved after the beginning of the Cambrian.

As discussed above, the Phanerozoic origin of several unconnected groups weakens the hypothesis that the echinoderm subphyla and classes differentiated in the Precambrian. The notion of extensive Precambrian differentiation is also weakened by the similarity of Early Cambrian echinoderms. Precambrian phylum- and class-level differentiation is an hypothesis inspired by seemingly large morphological differences between early Phanerozoic taxa. Unfortunately, the late Precambrian fossil record does nothing to support this hypothesis. I submit that the difficulty lies less with a faulty Precambrian record and more with inaccurate accounts of the early Phanerozoic record and inappropriate assumptions about morphological change during evolution.

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## 22. PRECAMBRIAN-CAMBRIAN REFERENCE SECTION IN MONGOLIA

By

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Recently, Precambrian-Cambrian boundary problems have been discussed in detail only for platform areas (such as the Siberian, East European, and South Chinese platforms). A lot of difficulties arise in Precambrian-Cambrian boundary determination in the geosynclinal regions. Sometimes it is very difficult to differentiate the Vendian and Tommotian levels because of the poor fauna or the lack of one or the other. Thus the Salany-Gol section (West Mongolia) is of great interest because a rich fauna has been found there. The Palaeontological Institute has carried out a special study which has resulted in the finding of rich complexes of ancient fauna, flora, and microphytolites that make it possible to place with confidence the Precambrian-Cambrian boundary and carry out a detailed subdivision of the Tommotian. This study is a part of the work of the Joint Soviet-Mongolian Palaeontological Expedition and Project 29 of the IGCP. The occurrence here of fossils that are widely distributed in the Siberian, East European, and South Chinese platforms makes this section not only interesting as a Precambrian-Cambrian reference section, but also important for correlation. The Salany-Gol section is located 65-70 km northwest of the town of Altay, on the northeast slope of the Khasagt-Khairkhan ridge. The Vendian-Cambrian deposits are carbonates and terrigenous carbonates and form a monocline with angles of dip equal to  $40^{\circ}$ - $60^{\circ}$ , somewhat complicated by small folds and faults of small amplitude. Lithologically, the Precambrian and Lower Cambrian rocks are subdivided, from oldest to youngest, into effusive rocks (the Dzabkhan Formation), dolomites and dolomitic limestones (the Tsaganolom Formation), terrigenous rocks with carbonate layers and lenses (the Bayangol Formation), biohermal limestones with thick conglomerates and breccia in the bottom (the Salanygol Formation), and terrigenous rocks which unconformably underlie biohermal limestones (the Khajrkhan Formation).

The age of the Tsaganolom Formation is determined by Yudomian microphytolites (Markova and others, 1972; Korobov and Missarzhevsky, 1977). The Bayangol Formation is characterized by a Tommotian

fauna from the very bottom at several levels, but the upper part of the Bayangol Formation probably belongs to the Atdabanian. Based on the fossils (gastropods, hyolithids, tommotiids, and phosphatic problematica), the terrigenous-carbonate deposits are subdivided into five parts, characterized by particular taxa: 1. Tiksitheca licis-Maikhanella multa; 2. Ilsanella compressa; 3. Anavarella plana; 4. Tannuella gracilais; and 5. Stenothecoides.

The assemblage of the faunal level with Tiksitheca licis-Maikhanella multa is not very diverse. Besides the "local" fossils, there are some Siberian forms which are typical of the lower part of the Tommotian Stage: Tiksitheca licis Miss., Cambrotubulus decurvatus Miss., Anabarites trisulcatus Miss., and Sachites sacciformis Mesh. The combination is most typical of the Aldanocyathus sunnaginicus Zone and the lower part of Dokidocyathus regularis Zone. In this assemblage are Tommotia aff. baltica Bengtson, Halkieriida, and Rozonoviella atypica Miss., which are also found in the lower part of the Tommotian Stage in the Olenek uplift of Siberia (Missarzhevsky, 1981).

The level containing Ilsanella compressa is characterized by the occurrence of diverse mollusks, namely Latouchella sibirica (Vost.), L. Korobkovi (Vost.), Anabarella exiqua sp. nov., and specimens of the genera Ilsanella and Barskovia as well as Lapworthella tortuosa Miss. Lapworthella tortuosa Miss. is typical of the lower part of Dokidocyathus regularis Zone of the Siberian platform. The Tommotian Age of this level is clear. It should be noted that this level contains typical fossils of the Yudomia-Olenek facies of the Siberian platform and the L. Korobkovi-A. plana Zone, which was considered by some scientists (V. E. Savitsky, 1971; Val'kov, 1975) to be more ancient than the Aldanocyathus sunnaginicus Zone.

The appearance of Anabarella plana Vost., a new species of Tannuella, and Bemella jakutica (Miss.) allows us to distinguish the level with Anabarella plana. This level is also characterized by the occurrence of the mollusks Halkieriida, Hyolithida, and Archaeooides. The appearance of Epiphyton is

important as well. This part of the section is correlated with the middle and upper parts of the Tommotian Stage.

The level with Tannuella gracilis has to a considerable extent the same assemblage of fossils as the underlying level with Anabarella plana but differs by the appearance of Tannuella gracilis and brachiopods of the genus Kundatella. At present this level is assigned conventionally to the Tommotian Stage, but there is a possibility that it can be referred to the Atdabanian.

The level with Stenothecoides is considered to be of Atdabanian Age because of the appearance of Stenothecoides. The majority of the fossils occurring in the underlying level are absent here. At this level there are acritarchs, among which the most interesting are Leiosphaeridia cerebriformis Volk., Baltisphaeridium varium Volk., and Pterospermopsimorpha. These acritarchs usually occur in the Talsy and even the Vergale assemblages of the East European platform.

The Salanygol Formation belongs to the Atdabanian and Lenian Stages. The age of this formation is determined on the basis of abundant archaeocyathids. The Alataucyathus jaroshevitchi Zhur.-Tabulacyathellus bidzhiensis Miss.-Pretiosocyathus subtilis Roz. assemblage, well known in the Altay-Sayan region, is typical of the lower (Atdabanian) part of the biohermal limestones. Dokidocyathus tuvaensis Roz., Soanicyathus admirandus Roz., Flindersicyathus latus (Vol.), and Syringocnemidae are found in the upper (Lenian) part of the biohermal limestones.

The Khajrkhas Formation is believed to be assigned to the Lenian Stage, but we can't rule out the possibility that these deposits are younger. The diverse fossils of this formation are contained in boulder conglomerates at several levels.

Thus the section in West Mongolia is of great significance for solving many problems of

Precambrian-Cambrian stratigraphy, and especially those of the Lower Cambrian. Its correlation with the Siberian and East European platforms is discussed above. The occurrence in the Salany-Gol section of a number of the forms first described from China allows us to recognize some stratigraphic similarity between the Mongolian and Chinese sequences. The comparison of the lowermost horizons of the Cambrian is of great interest. The deposits known as the Meishucun Stage cannot be more ancient than the Tommotian stage. In a number of sections of South China, the upper part of the Meishucun Stage could be Atdabanian.

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## 23. EUSTATIC CONTROL OF LITHOFACIES AND BIOFACIES CHANGES NEAR THE BASE OF THE TREMADOCIAN

By

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Intercontinental correlation of Tremadocian strata has been difficult because of strong lithologic and faunal contrast among coeval major depositional settings. An effort to solve this problem is being made by the Cambrian-Ordovician Boundary Working Group. The Working Group seeks to select a boundary stratotype section at which to standardize the Cambrian-Ordovician boundary. We report data here which we believe will improve our understanding of the depositional environments, stratigraphy, and faunas of strata near the base of the Tremadocian.

### TREMADOCIAN DEPOSITONAL SETTINGS

Analysis of Tremadocian sections from around the world suggests three major contrasting depositional settings: (1) low-latitude continental shelves and continental slopes, (2) high-latitude continental shelves and continental slopes, and (3) open-ocean floors, for which latitude was unimportant. Low-latitude shelf sequences include shallow-marine, high-energy, sometimes stromatolitic carbonates containing a diverse fauna of trilobites, articulate brachiopods, conodonts, and sessile dendroid graptolites. Low-latitude continental slopes often display mixed facies. In situ laminated carbonates contain many pelagic olenid trilobites, some conodonts, and horizontal anisograptids and occasional dictyonemid graptolites. Allochthonous carbonates containing shelf-derived faunas may be interbedded with fossiliferous in situ deposits (Cook and Taylor, 1975).

In sharp contrast to low-latitude carbonate sediments, high-latitude continental shelf and continental slope sediments contain sparse primary carbonate deposits. Instead, these strata consist mainly of coarse- to fine-grained clastics. Faunas consist of olenid and agnostid trilobites, rare conodonts, and a distinctive sequence of dictyonemid graptolites. Oceanic deposits are similar to high-latitude sequences both lithologically and faunally.

### DISTRIBUTION OF TREMADOCIAN FAUNAS

Late Cambrian and Tremadocian trilobites are widely distributed, but there are major differences among taxa from various environments. This factor has limited their use in intercontinental correlation, although they are extensively used for local and regional correlation. Within the North American craton, regional lithofacies changes may produce considerable variation in regional trilobite faunas. Intercratic differences are even more pronounced, as can be seen by comparing Upper Cambrian faunas from North America (Stitt, 1977), Siberia (Rozova, 1968), and Scandinavia (Henningsmoen, 1957).

Cook and Taylor (1975), Taylor (1977), and Taylor and Forester (1979) developed a model for early Paleozoic benthic trilobite distribution based on marine climate. Trilobites adapted to the cold, temperature-stable marine climates below the permanent thermocline had wide geographic distribution in deep-oceanic and high-latitude habitats, and in the deeper parts of low-latitude continental slopes. Benthic trilobites adapted to the warm and seasonally variable marine climates of low- and intermediate-latitude shelf seas found the cold waters of the deep ocean a barrier to migration.

Late Cambrian and early Tremadocian conodonts have been described relatively recently, and less is known about their geographic distribution than for coeval trilobites. Miller (1980) has summarized the occurrence of the euconodonts, but less is known of the distribution of paraconodonts. In low-latitude cratonic environments, primitive euconodonts replaced most paraconodonts during late Franconian or early Trempealeauan time. In other climatic regions the paraconodonts were common well into the Tremadocian. Adaptation to cold temperatures in these regions may have prevented migration of primitive euconodonts into low latitudes. Among Tremadocian euconodonts there is considerable variation in distribution of taxa. Some are apparently endemic to North America, some are known from several continents (such as the *Hirsutodontus simplex*, which is known from Australia, North America, and Siberia), and species of *Cordylodus* are apparently cosmopolitan.

The only graptolites known from pre-Tremadocian strata are sessile benthic forms with limited usefulness in biostratigraphy. The base of the Tremadocian is marked by the sudden appearance of planktic Dictyonema. Species and subspecies of this genus have been widely used for biostratigraphic correlation, but they have limited distribution. Dictyonema and Bryograptus possessed heavy rhabdosomes and apparently lived mostly in cool open-ocean areas and high-latitude shelf seas. Somewhat later, the horizontal anisograptids developed lighter rhabdosomes and became adapted to the warmer waters of low-latitude bathypelagic and neritic environments above the thermocline.

Not all of the factors controlling the distribution of Tremadocian faunas are known. However, in a general way faunas appear to have been closely tied to the three major environments discussed earlier. Water temperature, as related to depth and paleolatitude, appears to have been an important factor in faunal distribution. The most difficult problem in lower Tremadocian biostratigraphy seems to have been correlating zonal schemes based on cold-water trilobite-graptolite sequences, such as those from the Acado-Baltic Province, with schemes based on warm-water trilobite-conodont sequences, such as those from North America and Australia. An important step in correlating the base of the Tremadocian between these areas was made by Landing and others (1978). Their discovery of associated olenid trilobites, dictyonemid graptolites, and cordylodid conodonts led them to conclude that the Croixan Series-Canadian Series boundary in North America is approximately equivalent to the Upper Cambrian Series-Tremadocian Series boundary in the Acado-Baltic Province.

Correlation of Tremadocian strata is thus clearer than was the case some years ago, although our knowledge is far from complete. Regional zonal schemes based on environmentally controlled faunas can be used for intracratonic correlation. Intercratonic correlation is possible by utilizing widely distributed faunas such as olenid trilobites, graptolites, and conodonts. Thus it is possible to correlate widespread Tremadocian and equivalent sections representing diverse depositional environments. A correlation chart of 65 sections of Tremadocian strata from all of the present continents has been prepared by Erdtmann (unpublished). Although refinement of many of the correlations will surely occur, the chart can be used for regional interpretations.

#### ENVIRONMENTAL CHANGES AT BEGINNING OF TREMADOCIAN

Paleoenvironmental analysis of the worldwide Tremadocian Series and equivalents reveals widespread shifts in depositional environment near the beginning

of the Tremadocian. Just prior to the start of Tremadocian time, a small-scale eustatic drop in sea level occurred. Essentially at the start of Tremadocian time sea level rose again, perhaps to near its previous level. This event and the associated lithologic and faunal changes have been discussed by Miller, Stitt, and Derby (1977) and by Miller (1978, p. 16-21).

The eustatic drop in sea level occurred at the beginning of the Cordylodus proavus Zone, which corresponds exactly to the beginning of the Corbinia apopsis Subzone of the Saukia Zone (Miller, 1980). The drop in sea level changed the depositional environment of carbonate sections in Utah, Texas, Oklahoma, and Siberia, and of platform sequences in China. Oolitic or stromatolitic limestones or intraformational limestone conglomerates at the base of the Cordylodus proavus Zone represent higher energy conditions than in strata below, indicating a period of lowered sea level. Continental slope sequences from areas of high paleolatitude in segments of Gondwana or from the Baltic-Russian Platform also record this period of lowered sea level. The eustatic event is represented in northern Norway, western Turkey, the Podolian Platform, and South Korea by the interbedding of more or less massive quartz sandstones with pelitic laminarites. In northern Wales, Shropshire (Great Britain), the Montagne Noire (France), Morocco, Afghanistan, southern Anhui (eastern China), and Lancefield (Victoria, Australia), the eustatic sea level drop produced brief hiatuses.

The regression and brief low stand of sea level were followed by a transgression, which probably marks the base of the Tremadocian Series. In 25 of the 65 sections studied (mostly from low-latitude settings) the transgression is recorded by the resumption of carbonate deposition above disconformities. In two additional sections there is other evidence of disconformity. In 28 sections the transgression is manifested by a shift from coarse clastic to black shale deposition. In 10 sections consisting of black shale, there is uniform deposition throughout the Upper Cambrian-Tremadocian transition.

The cause of the brief marine regression and later transgression may be recorded in ancient Gondwana. Within the clastic marine lower Tremadocian Saladillo Formation of northwestern Argentina and in the Limbo Group of the Bolivian Cordillera Oriental, diamictites and striated cobbles are found. These features suggest a glacial event may have been responsible for the eustatic changes in sea level.

## FAUNAL CHANGES NEAR BEGINNING OF TREMADOCIAN

Changes in sea level near the beginning of the Tremadocian had drastic effects on marine invertebrates. These effects have been most thoroughly documented for North American trilobites, which suffered major extinction at the end of the Ptychaspid Biomere. Biomeres, originally defined by Palmer (1965), have been analyzed by Stitt (1971, 1977). They are, in effect, large biostratigraphic units similar to range zones but defined by trilobite families. Stitt (1971) divided the Ptychaspid Biomere into four evolutionary stages. In the first stage a new fauna of trilobites appeared on the craton, presumably having migrated from the open ocean. During the second and third stages the several families evolved into a stable and diverse fauna. At the start of stage four of the biomere, a crisis caused extinction of most of the common species and many of the genera of trilobites. New species of preexisting genera appeared along with a few olenids. The fauna of stage four was short lived, and at the end of this stage virtually all of the trilobite species, genera, and families became extinct. Soon new families of trilobites migrated into the area and began to diversify.

The extinction of trilobites at the base and top of Stitt's stage four are closely related to the eustatic sea-level changes discussed above. The first extinction is at the beginning of the Corbinia apopsis Subzone and corresponds to the eustatic drop in sea level. The glaciation in Gondwana caused a drop in sea level and a migration of cold water onto low-latitude continental shelf areas (Stitt, 1977, p. 23-24). Trilobites adapted to warm water became extinct, and new species, which could cope with the cold conditions quickly evolved. The newly arrived olenids were already well adapted to the cold water. The second extinction, at the top of the C. apopsis Subzone and the top of the biomere, apparently occurred at the start of the eustatic sea level rise and resulting transgression. The second extinction may have reflected the ultimate inability of the C. apopsis Subzone fauna to cope with the cold conditions, or it may have been caused by the return of warmer water to the shelf area during transgression. The transgression brought with it a new fauna, found in the Missisquoia Zone. The base of the Missisquoia Zone marks the base of the Canadian Series and the base of the Ordovician System in North American usage. Similar biomere changes can be recognized in Siberia and Australia.

Other North American faunal elements also reflect these eustatic changes. The drop in sea level and influx of cold water caused the extinction of most of the Proconodontus Zone conodont fauna (Miller, 1980). The Cordylodus proavus Zone fauna appeared during the time of lowered sea level. The later rise of

sea level caused no extinctions, only a several-fold increase in conodont abundance. Similar changes in conodont faunas occur in Australia.

The faunal change is different in cold-water environments. There are only modest changes in the basal Tremadocian olenid trilobite faunas in Scandinavia (Henningsmoen, 1957). The major faunal change in the cold-water environments was the sudden appearance of the planktic graptolite Dictyonema, corresponding with the rise in sea level at the base of the Tremadocian. As noted earlier there was widespread deposition of black shale at this time. This lithology may demonstrate that these areas were invaded by cold, oxygen-poor water. This water migration may have played a role in the evolution of planktic habitat among the graptolites. The new graptolites may have exploited oceanic phytoplankton blooms resulting from the expansion of nutrient-rich anoxic water masses during the early Tremadocian transgression.

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## 24. UPPER CAMBRIAN BIOSTRATIGRAPHY OF THE KYRSHABAKTY SECTION, MALY KARATAU, SOUTHERN KAZAKHSTAN

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A number of Upper Cambrian biostratigraphic schemes have been proposed (Westergaard, 1922, 1944; Howell and others, 1944; Ivshin, 1956, 1962; Ivshin and Pokrovskaya, 1968; Henningsmoen, 1957; Lochman-Balk and Wilson, 1958; Pokrovskaya, 1961; Savitsky, 1959; Palmer, 1962, 1965; Palmer and Taylor, 1976; Opik, 1963, 1967; Lazarenko, 1966; Lazarenko and Nikiforov, 1972; Rosova, 1964, 1968; Cowie and others, 1972; Shergold, 1975). However, no general Upper Cambrian zonal and stage scale has been worked out yet because of lack of a key section. Data from the Kyrshabakty section are relevant to the development of a general stage and zonal scale for the Upper Cambrian. This section is important primarily because it contains a continuous sequence from the lower Middle Cambrian through the Lower Ordovician and consists mainly of carbonate facies of an open shelf, which contain a rich and diversified fauna of more than 10 taxonomic groups, with the trilobites prevailing. Fossil genera and species present represent all the paleogeographic regions of the world. This is most important for the stratigraphy and world wide correlations. The abundance of the familiar taxa, agnostids particularly, demonstrates extensive connections between the Karatau paleobasin and the world ocean. Indeed, faunal the migration between the Atlantic and Pacific provinces of Cambrian and Ordovician time must have been through the Karatau region. This is proved by the association of many trilobite taxa characteristic of Scandinavia and Siberia as well as China, Korea, Australia, and North America. The present section contains at least 18 biostratigraphic zones and deserves to become a stratotype for the upper division of the Cambrian System.

The study of the trilobites from this section allows us to elaborate on the the stage and zonal scale for the Middle and Upper Cambrian, and tentatively for the Lower Tremadocian, based on the evolutionary changes of trilobite associations, and also to define the extent and limits of subdivisions and make intercontinental correlations. Altogether 20 zones have been distinguished in the Kyrshabakty section according to genetically closely related trilobite associations, and these zones are grouped into six stages: Amginian, Mayanian, Ajusockanian, Sackian, Malykaratauan, and Tremadocian (Ergaliev, 1979, 1980).

Definitions of zones and stages are discussed in our publications in detail. It is worth mentioning that the zone boundaries have been defined based on the first appearance, gross evolution, and disappearance of diagnostic agnostids, specific new agnostid complexes, and polymerids.

A brief characterization of subdivisions corresponding to the Upper Cambrian and boundary beds is shown in figure 1. The range chart shows only trilobites and conodonts. Conodont identifications are by G. P. Abaiomova and T. B. Baytorina. The remainder of the faunas are unstudied. According to S. P. Koneva, who studied the inarticulate brachiopods, no detailed brachiopod zonation is possible, because the taxa have long vertical ranges. However, based on changes in associations, the boundaries between larger subdivisions, such as systems, divisions, and stages, may be recognized (see fig. 1). According to G. P. Abaimova, the conodonts do not allow subdivision of the Middle and Upper Cambrian into minor units.

The Mayanian Stage, consisting of three zones, rests directly above the Ptychagnostus intermedius Zone, which represents the upper Amginian Stage according to its fauna. The upper boundary of this stage does not coincide with the traditional stratotype boundary, as it is confined to the base of the Lejopyge laevigata Zone, which marks a new step in the trilobite evolution expressed by the appearance of the earliest members of the family Anomocariidae and species of Hypagnostus, Fuchouia, and others.

The Goniagnostus nathorsti Zone is characterized by a diversity of agnostids and polymerids, a number of which are transitional; many of them appear for the first time: Goniagnostus nathorsti (Brøgg.), G. longispinus Pokr., Clavagnostus repandus (West.), Prodamesella convexa Chang, and several species of Hypagnostus, and Lisania. Pseudophalacroma dubium (White.), Ps. crebra Pokr., Phoidagnostus orbiculatus Erg., Fuchouia spinosa Lu, and Lisania bura Walc. are taken as guide fossils. Thickness is 16.5 m.

The Lejopyge armata Zone is recognized by a diversity of agnostids dominating over polymerids. The zone is closely related to the underlying and overlying zones, as it contains many forms that cross the lower and upper zone boundaries.

Most of the species disappear at this level; newcomers spread widely through the Lejopyge laevigata Zone and up the section. Lejopyge armata

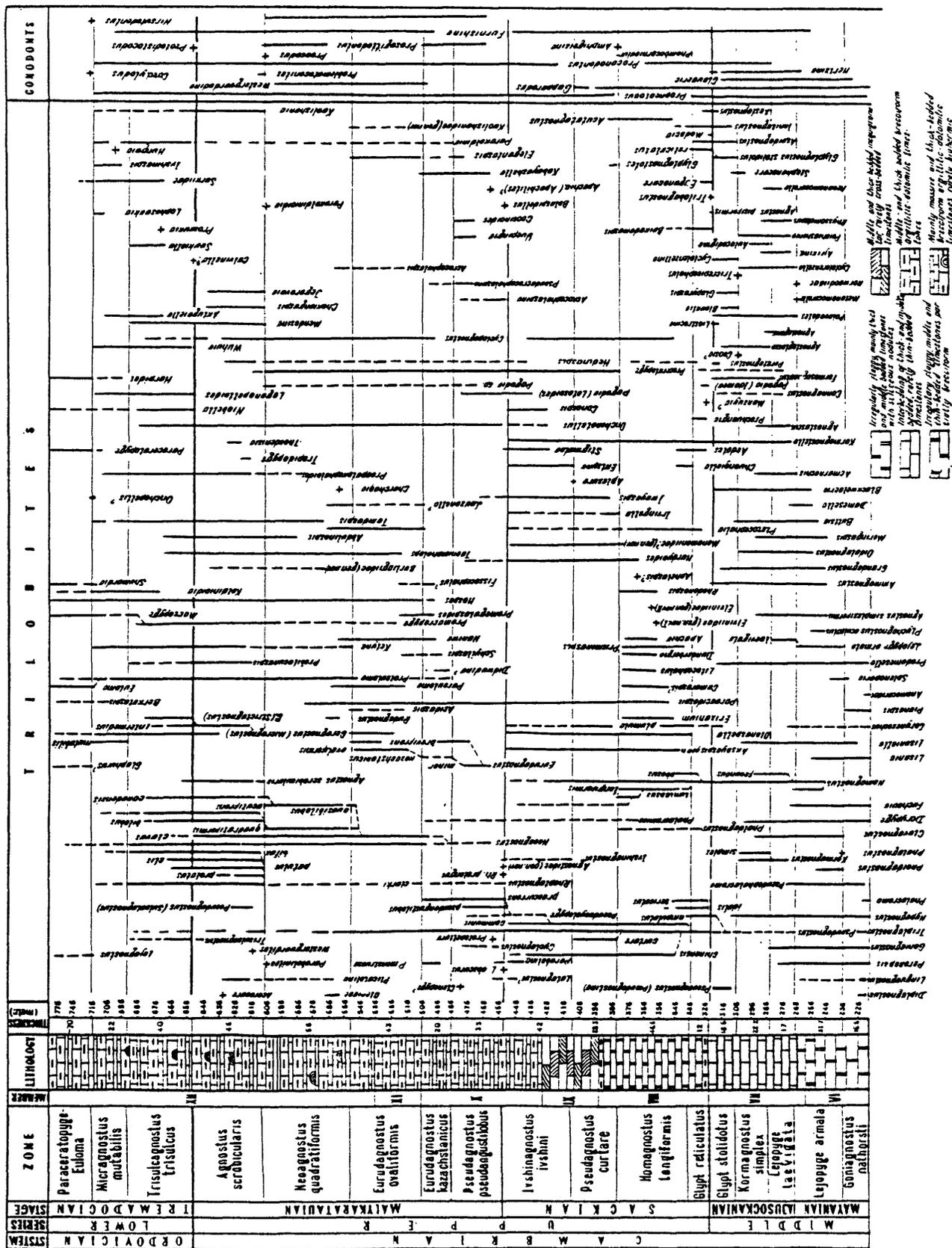


Figure 1.--Range of trilobites and conodonts in the Kyrshabakty section, Maly Karatau, southern Kazakhstan.

(Linnrs.), Ptychaagnostus aculeatus (Ang.), Goniagnostus longispinus Pokr., Linguagnostus tricuspis Lerm., Lejopyge calva Rob., Homagnostus pater West., Damesella sp., and Blackwelderia ex gr. paronai (Ajrachi) characterize the zone. Thickness is 31.7 m.

The Ajusockian Stage embraces three zones; it overlies the Lejopyge armata Zone and underlies the Glyptagnostus reticulatus Zone. This part of the Kyrshavakty section seems to be the stratotype of the stage. The stage is characterized by a major development of Damesellinae, Drepanurinae, Aulocodigmatidae and several agnostids: Kormagnostus, Ammagnostus, Acmarhachis, Agnostascus, and Agnostoglossa (see fig. 1). The upper boundary of the stage is located at the base of the Glyptagnostus reticulatus Zone because of the appearance of both new species and a number of families and subfamilies (Pagodidae and Pterocephalidae). Thickness is 58 m.

The Lejopyge laevigata Zone overlies the Lejopyge armata Zone, which is proved by the coexistence of armata and laevigata in its lower part. Besides, species of Acmarhachis, Pseudagnostus (Pseudagnostus), Kormagnostella, Grandagnostus, Ajrikina, Cyclolorenzella, Peichiashania, Palaeadotes, Proceratopyge, and Norwoodidae make their first appearance beginning near the base of this zone; whereas Homagnostus fecundus Pokr. and Erg. and Blackwelderia sinensis (Berger.) attain acmes in the succeeding zones. Lejopyge coss, Ammagnostus psammius, Acmarhachis quasivespa, Oidalagnostus trispinifer (West.), Peichiashania bispina Erg. and Lisaniella elongataformis Erg. are common in this zone. Thickness is 17 m.

The Kormagnostus simplex Zone is also characterized by a diversity of agnostids and polymerids, most of which do not disappear at this level; some of them range into the overlying Glyptagnostus stolidotus Zone. Kormagnostus simplex Röss., Acmarhachis karatauensis Erg., Formosagnostus Erg., Clavagnostus bisectus O., Agnostoglossa bassa O., Hypagnostus correctus O., Palaeadotes angustus Erg., Prodamesella punctata Erg., and other forms also characterize this zone. Thickness is 22 m.

The Glyptagnostus stolidotus Zone is characterized by a transitional fauna consisting of both the "Upper Cambrian" and "Middle Cambrian" taxa, the latter of which--Hypagnostus, Grandagnostus, Prodamesella, and Peichiashania--are believed to become extinct here. Coosia? sp., Tricrepicephalus sp., Blountia sp., Innitagnostus innitus O., Aspidagnostus sp., Pseudagnostus (Pseudagnostus) ampullatus O., and Ps. (Ps.) karatauensis Erg. appear for the first time, whereas Glyptagnostus reticulatus angelini Röss. ranges into the next zone above. Glyptagnostus stolidotus O., Pseudagnostus (Pseudagnostina) pseudodouvillei Erg., Peratagnostus nobilis O., Hypagnostus durus O., Liostracina krausei

Monke, Cyclolorenzella conifrons Erg., and Glaphyraspis parviformis Erg. are common in this zone. Thickness is 18.5 m.

The Sackian Stage consists of four zones, which together are taken as a stratotype of the stage. The genera and species in this stage (except the zonal guide species) are as follows: Innitagnostus inexpectans (Kob.), Homagnostus obesus (Belt.), H. tumidosus (Hall and Whit.), Aspidagnostus rugosus Palm., Glyptagnostotus elegans Laz., Peratagnostus nobilis O., Pseudagnostus (Pseudagnostus) idalis O., Ps. (Ps.) communis (Hall and Whit.), Acutatagnostus, Ivshinagnostus, Irvingella, Euganocare, Aedotes, Pagodia (Idamea), Stigmatoa, Dunderbergia sp., and Pterocephalina sp. (see fig. 1).

The boundary between this stage and the overlying Malykaratauian Stage is defined at the base of the Pseudagnostus pseudangustilobus Zone by the appearance of all above listed taxa.

The Glyptagnostus reticulatus Zone is distinguished by the occurrence of the index species in association with a late Late Cambrian agnostid-polymerid community. Glyptagnostus reticulatus is joined here by Aspidagnostus rugosus Palm., A. strictus O., Agnostus pisiformis (L.), Pseudagnostus (Pseudagnostus) idalis O., Ps. (Ps.) karatauensis Erg., Innitagnostus inexpectans (Kob.), Proceratopyge nathorsti West., Euganocare cf. tesselatum Whiteh., Baikadamaspis Erg., and other transitional forms (see fig. 1). Thickness is 12 m.

The Homagnostus longiformis Zone is characterized by a very rich trilobite assemblage mainly of polymerids. The most common forms are Homagnostus obesus (Belt.), H. longiformis Erg., H. tumidosus (Hall and Whit.), Acutatagnostus acutatus Erg., Pseudagnostus (Pseudagnostus) communis (Hall and Whit.), Ps. (Ps.) chinensis (Dames), Phalacromina minor (Kob.), Cycloagnostus asper Laz., Prismenaspis trisulcatus Erg., Erixanium carinatum Palm., Litocephalus sp., Paraacidaspis hunanica Jegor., Chuangiella sp., Pterocephalia sp., a new genus of Elviniidae, and some transitional species and genera (see fig. 1). Thickness is 46.6 m.

The Pseudagnostus curtare Zone differs in the predominance of various polymerids compared to agnostids. Peculiar forms are Pseudagnostus (Pseudagnostus) curtare Hend., Glyptagnostotus elegans Laz., Phalagnostus orbiformis Ivsh., P. absurdus Erg., Homagnostus paraobesus Lerm., H. claviformis Erg., Olenaspella borealis (Lerm.), O. consimila Erg., and Proceratopyge fragilis (Troed.) (see fig. 1). Thickness is 28.5 m.

The Ivshinagnostus ivshini Zone is recognized by a diverse fauna of polymerids and agnostids. Many of them range upward from the underlying zones and become extinct here. The other forms are unique to this zone, and only a few of them range higher. The guides for this zone are Ivshinagnostus ivshini Erg.,

Homagnostus cf. ultraobesus Lerm., Pseudagnostus (Pseudagnostus) chinensis (Dames), Irvingella major Ulr. and Ress., Stigmatia sidonia O., Aplexura sp., and Entsina sp. (see fig. 1). Species and genera such as Pseudagnostus (Pseudagnostus) pseudocyclopyge Ivsh., Onchonotellus abnormi Ivsh., O. perlatum Ivsh., Proceratopyge asiatica Ivsh., Hedinaspis sp., Parabolina sp., and other forms occur sparsely in the upper part of the zone but attain their maximum development in the next zone above. The members of the genus Homagnostus and Pseudagnostus (Pseudagnostus) communis (Hall and Whit.), Ps. (Ps.) chinensis (Dames), the Pteroccephalidae, and the Elviniidae are not known above this zone. Thickness is 42 m.

The Malykaratauian Stage is defined as embracing five zones being located between the Sackian and Tremadocian Stages. This interval is thought to be a stratotype of the Malykaratauian Stage. Lotagnostus, Rhaptagnostus, Neoagnostus, Eurudagnostus, Parabolina monstruosa, Plicatolina, Promacropyge, Acerocare, Westergaardites, Acrocephalaspina, Pseudacrocephalaspina, Hedinaspis, Chekiangaspis, and Jegorovaia (fig. 1) are typical of the stage. The boundary between the Malykaratauian Stage and the overlying Tremadocian is defined at the base of the Trisulcagnostus trisulcus Zone. Many taxa that predominate in the Malykaratauian Stage do not range into the I. trisulcus Zone (Pagodia, Kobayashella, Hedinaspis, Proceratopyge, Pelturinae, and others), whereas the Saukiidae, Ptychaspidae, Loganopeltinae, and other forms make their first appearance in this zone (see fig. 1). Thickness is 196 m.

The Pseudagnostus pseudangustilobus Zone is marked by the appearance of Rhaptagnostus, Neoagnostus, Cyclagnostus elegans Lerm., Eurudagnostus minor Erg., numerous Acrocephalaspina, Onchonotellus, Hedinaspis, and new species of the genera Pseudagnostus (Pseudagnostus), Proceratopyge, and others (see fig. 1). Thickness is 33.6 m.

The Eurudagnostus kazachstanicus Zone differs in having more diverse polymerids and monotonous agnostids. The zone is closely related to the zones above and below, as many forms are transitional. The following taxa characterize the zone: Eurudagnostus kazachstanicus Erg., Pseudagnostus (Pseudagnostus) praecurrens Erg., Parabolina monstruosa Pokr., Iwayaspis asaphoides Kob., and Pseudacrocephalaspina strabiliformis Erg. (see fig. 1). Thickness is 20.5 m.

The Eurudagnostus ovaliformis Zone is defined by the unique association of trilobites such as Eurudagnostus ovaliformis Erg., Neoagnostus clavus (Sherg.), N. cyclopygeformis (Sun), Eurudagnostus brevifrons, E. ovaliformis Erg., Geragnostus (Microagnostus) spinosa (Chien), Promacropyge amboliti (Troed.), Kaolishaniidae (new genus), and Elegantaspis sp. Many species of Proceratopyge vanish here (see fig. 1). Thickness is 43 m.

The Neoagnostus quadriformis Zone is characterized by the refreshed agnostid-polymerid assemblage. In addition to the guide forms, species recognized include Neoagnostus vulgaris (Ros.), N. quadriformis Erg., Rudagnostus rudus (Salt.), Taenicephalops kyrshabactensis Erg., Pareuloma sp., Hospes limbatus Erg., Olenidae gen. and sp. indet., Ketyna karatauensis Lis., Abdulinaspis concinus Erg., and Proapatokephalinoidea longiformis Erg. are recognized. Tamdaspis and other forms first appear (see fig. 1). Thickness is 55 m.

The Aagnostus scrobicularis Zone is distinguished by an incursion of genera and species of agnostids and polymerids. Many forms disappear at this level below the upper third of the zone. This zone is characterized by Aagnostus scrobicularis Erg., Pseudagnostus (Sulcatagnostus) rugosus Erg., Neoagnostus bilobus (Shaw), N. quasibilobus (Sherg.), Rhaptagnostus clarki prolatus (Sherg.), Acerocare sp., Westergaardites pelturaeformis Troed., Plicatolina partita (Liz.), Parabolinites bisulcatus Erg., Promacropyge carinata Lu, Chekiangaspis chekiangensis Lu, Jegorovaia expansa Lu, Mendosina cf. laciniosa (Sherg.), Proteuloma debila Erg., and Tamdaspis tamdensis Lis. (see fig. 1). Thickness is 45 m.

The Tremadocian Stage (the lower part), consisting of three zones, is recognized above the Aagnostus scrobicularis Zone. The Stage yields Acerocare, Westergaardites, and others. The characteristic taxa of this stage are mainly Geragnostus (Micragnostus), Saukiella, Wuhuia, Loganopeltoides, and Ivshinaspis; abundant Ketyna, Proteuloma, Probilacunaspis, and Aktugaiella; and rare Harpides, Euloma, and Paraceratopyge. This association is similar to that of the Upper Cambrian Trempealeauan Stage of North America and its equivalents. The thickness of the strata conforming to the upper Tremadocian is about 66 m in the Kyrshabakty Mountains and on the order of 130 m along the Batyrbasay ravine.

The Trisulcagnostus trisulcus Zone is recognized by the markedly replenished trilobite association, represented by Late Cambrian and Early Ordovician genera and species. Here a specific trilobite association is present with abundant Geragnostus (Micragnostus) intermedius (Palm.), Neoagnostus bilobus (Sherg.), N. quasibilobus (Sherg.), N. canadensis (Bill.), Rhaptagnostus bifax (Sherg.), Ketyna ketiensis Ros., Niobella kozchuchensis Petr., Probilacunaspis similis Erg., Aktugaiella acuminulata Erg., and others (see fig. 1). Thickness is 40 m.

The Micragnostus mutabis Zone contains a very rich but specific trilobite association in which agnostids decrease sharply. Wuhuia angustatus Erg., Loganopeltoides proprius Erg., Lophosaukia rectangulata Erg., Kaolishania australis Sherg., Ivshinaspis crispa Petr., Harpides sp., and Hunagaia sp. predominate (see fig. 1). Thickness 22 m.



The "Paraceratopyge-Euloma" Beds crown the Lower Tremadocian section, but only the lower part of is present in the Kyrshabakty section. The main part of the section is located in the area of the Shabakty River and Batyrbasay ravine; it presents a natural extension of the entire Kyrshabakty stratotype. Trilobites from this level are still under study; the identified forms are Geragnostus (Micragnostus) sp., Neoagnostus sp., Euloma sp., Niobella baikadamica Lis., Paraceratopyge asiatica sp. nov., Shumardia sp., Proteuloma cf. aksaiensis Lis., Berkutaspis sp., Onchopeltus sp., and Glaphurus? sp. (see fig. 1). It should be noted that Saukiidae are lacking and agnostids are rare; therefore this complex differs from that of the underlying zone. This zone is similar to the underlying zone in having many transitional forms, by which it was assigned to the lower Tremadocian.

The limited span of this report does not allow discussion of the question of the upper and lower boundaries of the Upper Cambrian and correlations with other regions; however, my publications contain extensive information on this point and offer some alternative ways of solving this complicated problem. The bases of the Glyptagnostus stolidotus and Micragnostus mutabilis Zones seem the most reasonable levels for drawing the boundaries.

The proposed zonal scale of the upper Middle Cambrian, Upper Cambrian, and lower Tremadocian in Maly Karatau may be correlated closely with the well known synchronous scales of the equivalent strata in the U.S.S.R. and abroad because 85 percent of the described genera and more than 45 percent of the species common to all the paleozoogeographic regions occur here. The correlations are shown in figure 2.

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## 25. PALAEOICHOLOGY OF THE PRECAMBRIAN-CAMBRIAN TRANSITION

By

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Trace fossils of invertebrates are one of the few kinds of fossils whose stratigraphic ranges embrace the Precambrian-Cambrian boundary. That is why we attach much importance to this group of fossils, although usually the stratigraphic significance of trace fossils is not considered high. On the other hand, the heuristic value of trace fossils for palaeoecology is well known. They are especially important for revealing the earliest stages of metazoan evolution. Traces may well allow determination of the time of first appearance of benthonic metazoans in the geological record, and may contribute considerably to the history of colonization by animals of the sea floor as habitat and ecological niche.

Recognition of most ancient trace fossils is an important but difficult task, as most Precambrian traces are rare and their morphology is simple. This is why we often doubt their biological origin. A skeptical attitude is increased also as a result of noncritical description of numerous pseudofossils as metazoan remains or trace fossils from Precambrian deposits.

The Vendian seems to be a peculiar stage in the long process of seafloor colonization. The great majority of Precambrian trace fossils have been described from Vendian deposits. After the period of global Laplandian or Varangerian glaciation, when the shelf zone was narrow and the life was concentrated mainly in the pelagic area, an epoch of great transgression, gigantic epiplatform seas, and vast shelf zones came into existence. Extended littoral zones characterize this period, as a result of intensive denudation of the land. Under these absolutely new environmental conditions, there happened one of the most important evolutionary explosions in terms of diversity and abundance in the record of the Metazoa. Palaeontologically, this explosion is documented by numerous remains of soft-bodied fauna and by trace fossils.

The Russian platform is rich in Vendian organic remains, and stratigraphically this region is well investigated. About 60 species of Precambrian metazoans and 20 forms of trace fossils have been described from the north of the platform (White Sea region) and from its southwest part (the valley of the Dniester in Podolia). Vendian trace fossils indicate a high level of organization of the vagile benthos of this

period. In the sediment, these animals moved by means of peristaltic changes of the body, like recent Annelida and Sipunculida, and some of them let the organic rich detrital sediment pass through their intestines. But a greater part of Vendian vagile benthos lived on the surface of the sediment or just beneath the sediment-water interface, moving by means of peristaltic waves passing along the ventral part of the body, like recent Turbellaria and Gastropoda. More rarely, they moved by means of lateral bending of the body, or with the participation of appendages.

Trace fossils usually cannot be correlated with any species of metazoans known by imprints. This fact emphasizes the special palaeontological importance of trace fossils. Vendian ichnocoenoses are characterized by relatively scanty bioturbations, which as a rule are small. Horizontally oriented *Pascichnia* and *Fodinichnia* are dominant. Biological processing of the sediment is usually low, although the density of benthic populations, especially in the littoral facies, can be high. The deepest burrows among Vendian trace fossils are dwelling-burrows, in particular thin inclined *Skolithos*(?) slightly tapering down, whose length is 40 mm, and whose diameter is no more than 2 mm.

One of the peculiarities of Vendian ichnocoenoses is trace fossils with repeated elements of symmetry. These trace fossils were formed by systematic repetition of similar motions in the process of nutrition, for optimal envelopment of the sediment (such as *Harlaniella*, *Palaeopascichnus*, *Nenosites*). Such traces are widespread in Vendian deposits, and indicate stable and inheritable behavioral programs. Identical forms are associated with Ediacara-type faunas in widely separated regions--for example, in the European part of the USSR and in South Australia. Thus, Vendian trace fossils can be used for stratigraphic correlation.

Ichnocoenoses change sharply in the Vendian-Cambrian transition, at the level of the maximum occurrence of Sabelliditidae in the Russian platform (Rovno Horizon). This change is represented by a higher degree of biological processing of sediments. Many new forms are large and penetrate deeply into the sediment. The diversity of morphologically

complicated trace fossils increases. Feeding traces with repeated elements of symmetry become widespread. Among them, in addition to subhorizontal bioturbations, there appear vertically oriented two-dimensional (Teichichnus) and three dimensional (Gyrolithes) systems nontypical of Vendian ichnocoenoses.

The colonization of the seafloor in the Vendian-Cambrian transitional period possibly became more intensive as a result of the stress of several biotic or abiotic factors. One can suppose that there was a strong competition among species when the density of benthic populations was growing. We also can assume that animals penetrated more deeply into the sediment because increasing oxygen content in the atmosphere improved conditions of aeration, and because more active (compared with the Vendian) utilization of

organic remains by various reducers in many cases excluded H<sub>2</sub>S contamination of the sediment and water near the floor, and made favourable an active occupation of ecological niches in this zone.

Beginning with the Atdabanian level of the Lower Cambrian, arthropod trace fossils dominate the shallow-water ichnocoenoses, although resting and crawling traces tentatively related to arthropods occur rarely in Tommotian deposits.

There is a striking similarity among Lower Cambrian ichnocoenoses in the different regions of the world. We can enumerate many forms that occur in the Vendian-Cambrian transitional zone in the same sequence. Such abundance of forms allows us to consider trace fossils as useful markers of the Precambrian-Cambrian boundary where one of the most important events in the history of the marine benthos is represented.

## 26. PRECAMBRIAN FAUNA OF THE RUSSIAN PLATFORM

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The Vendian, established more than 30 years ago as the youngest Precambrian sedimentary complex of the Russian platform, now is considered to be a complete stratigraphical system (680 $\pm$ 20 to 570 $\pm$ 10 m.y.). The main Vendian elements are tillite-bearing deposits of the Vilchan Series at the base, volcanic-clastic beds of the Volhyn Series, and terrigenous deposits of the Valdai Series. One of the characteristic features of the Vendian organic world is the record of soft-bodied multicellular animals whose remains and traces of life activity are known on other continents in the same stratigraphic position; that is, above the tillites of the last Precambrian glaciation and below the zone of mass distribution of Lower Cambrian skeletal faunas of the Tommotian Stage.

The richest associations of Vendian soft-bodied metazoans in the Russian platform are confined to the Valdai Series, and in particular to its lower Redkino Horizon. Within the last 10 years, we have discovered new localities of nonskeletal faunas in outcrops of the Valdai Series in the north of the platform (White Sea region) and in its south-western part (the valley of the Dniester in Podolia).

The best outcrops, with abundant metazoan imprints and trace fossils, are in the Zimnii Shore of the White Sea north-east of Archangelsk, and on the Omega Peninsula. There we discovered approximately 60 species of invertebrates. The Vendian White Sea biota is represented by an association of benthonic, planktonic, pleustonic, and nektonic organisms that belong to at least six phyla of Metazoa. A great majority of the animals were soft-bodied, and did not have any mineralized skeletal elements, although some forms show sclerotization of some organs and tissues.

Coelenterata constitute the most numerous group of Vendian organisms (about 70 percent of the species now described). They are characterized by large sizes (as much as to 50 cm or more) compared with representatives of other groups. Coelenterata are represented by various hydroid polyps, both solitary (Nemiana, Tirasiana, Beltanelliformis, Cyclomedusa, Pinegia, Paliella) and colonial (Ramellina, Zimniella, and possibly Charnia). Medusoids seem to be more rare. Among them there are hydroid (Nimbia, Protodipleurosoma) as well as scyphoid ones (Albumares). The most primitive

cyclomeroous Coelenterata demonstrate asexual reproduction, such as some kinds of budding and fission. The group of pleustonic organisms is represented by possible chondrophorans (Ovatoscutum and Eoporpita). There are grounds to suppose the existence Anthozoa in the Vendian, including solitary (Bonata) as well as colonial ones. In addition, the group of Coelenterata includes organisms of uncertain systematic position, which often are united under the name Petalonamae (Pteridinium, Inkrylovia, Archangelia, etc.).

Platyhelminthes constitute about 15 percent of the described species, and embrace representatives of the family Dickinsoniidae-5 species of the flat, leaf-shaped organisms with a metamerised integument or body; but other forms with a smooth body are also found.

Annelida are represented by unusual forms. Omega resembles the larvae of arthropods or onychophorans, and Spriggina is similar to arthropods in its type of cephalization.

Three forms (Vendomia, Parvancorina and Pseudovendia) can be assigned with some assumptions to the phyla Arthropoda. The enigmatic genus Tribrachidium possibly could be assigned to the Echinodermata, but phylogenetically rather than taxonomically.

A curious phenomenon characterizes the White Sea biota as a whole. Although the organization of the animals becomes more complicated from Coelenterata to Arthropoda and Echinodermata, specific diversity of animals, their quantity and body dimensions decrease. This phenomenon is to some extent a function of decreasing dimensions and taphonomic peculiarities of various groups, but undoubtedly it represents the early history of development of the main invertebrate phyla, among which Coelenterata are the most ancient.

The Vendian biota of Podolia discovered 15 years ago now has new finds made in the base of the Valdai Series (Lomozov Beds of the Mogilev Formation). The evolution of this fauna is identical to that of the White Sea and Ediacaran fauna. Among the 25-30 species found here, there are many taxa in common with the White Sea and Ediacara assemblages: Cyclomedusa, Medusinites, Conomedusites, Eoporpita, Pteridinium, Dickinsonia, Tribrachidium, and others. The discovery

of such a diverse fauna in the lower part of the Valdai Series allows us to suppose the existence of a significantly differentiated animal kingdom in pre-Valdai and probably pre-glacial times. This supposition should stimulate search for faunas in the Lower Vendian and pre-Vendian deposits. The stratigraphic sequence of Podolia is of great importance because the Vendian here is overlapped by the most ancient palaeontologically well-documented Cambrian deposits (the Baltic Series, with the Rovno Horizon at the base, which is characterized by abundant Sabelliditidae). This sequence is proposed to be one of the best reference sections of the Vendian on the platform, although the upper part of Valdai Series here contains only trace fossils.

Trace fossils associated with imprints of soft-bodied Metazoa are indicative of a high organization of vagile benthos among which possibly were annelids and mollusks. Grazing traces show the existence of rather complicated behavioral programs in the nutrition process. About 20 forms of trace fossils are described now from the Vendian of the Russian platform, but few of them can be correlated with metazoans known by their imprints.

On the whole, the following features are characteristic of the Metazoa of the Vendian biota that preceded the Cambrian biota:

1. Lack of mineralized skeletal elements.
2. High morphological diversity.
3. Differentiation at the level of high rank taxa.

4. Strong prevalence of Coelenterata.
5. Presence of all main ecological groups.
6. Conjoinement of benthos to the shallow-water environment.
7. Similarity of Vendian faunal associations all over the world as a result of the absence of essential ecological barriers during the gigantic post-glacial transgression.
8. Occurrence of specific (possibly transitional in the evolutionary sense) groups that are characterized by a combination of the features typical of different high rank taxa.
9. Presence of adult forms similar in body plan to the larval stages of organisms of younger geological ages.
10. Decrease of body sizes while the organization of animals is becoming complicated (larger forms occur among the most primitive animals, and forms of highest organization have usually the smallest dimensions).
11. First appearance of tissue sclerotization on the basis of organic matter in some groups of animals.
12. Lack of evident ancestors of the small shelly organisms and other groups of Tommotian fauna that appeared explosively in the palaeontological record due to skeletization.

## 27. FOSSILIFEROUS CAMBRIAN SEQUENCES IN THE SOUTHWESTERN PACIFIC PART OF GONDWANALAND

By

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Fossiliferous Cambrian sequences are known from several parts of the present southwestern Pacific part of Gondwanaland. In the Cambrian, these areas (northern and southern Victoria Land of Antarctica, New Zealand, Tasmania, Victoria, South Australia, and western New South Wales) were in close proximity, although the exact continental reconstructions have been the subject of some discussion (Laird and others, 1977, Jago, 1980). The Cambrian sequences have provided the key to the reassembly of this part of Gondwanaland because abundant fossiliferous sequences from other geological periods are absent. All Cambrian faunas in this part of Gondwanaland show asiatic affinities (Palmer, 1972).

The fossiliferous Cambrian sequences of this area can be divided into two major groupings:

1. Areas of essentially Early to Middle Cambrian sedimentation, where archaeocyathid-bearing shallow-water carbonate sediments, deposited on stable shelves are abundant; that is, southern Victoria Land, southern South Australia, and western New South Wales. These areas have been correlated mainly by means of archaeocyaths and polymeroid trilobites.
2. Areas of essentially Middle and Upper Cambrian clastic sediments deposited in more tectonically active areas and associated with Lower to Middle Cambrian volcanics; that is, northern Victoria Land, New Zealand, Tasmania, and Victoria. These areas have been correlated by the use of trilobites, particularly the agnostoids.

### LOWER TO MIDDLE CAMBRIAN SEDIMENTS

Southern Victoria Land: In the Nimrod Glacier area, probable late Proterozoic metasediments are overlain unconformably by the apparently 8000-m-thick Shackleton Limestone (fig. 1, col. 1), which contains archaeocyathids and trilobites. Archaeocyathids from 1000-1300 m above the base are of late Early Cambrian age, equivalent to the Botoma Stage of the Siberian Platform. The highest

archaeocyathids in the Shackleton Limestone are 5000 m above the Botoma archaeocyathids, hence suggesting structural repetition of the Shackleton Limestone (Laird, 1963). Certain archaeocyathid genera seem to be endemic to the Antarctic-Australian region (Jago and Gravestock, 1980).

Southern South Australia: The Cambrian sediments of southern South Australia were deposited in the Adelaide geosyncline around the eastern and southern margins of the Archaean to middle Proterozoic Gawler block, and also around the margins of the Proterozoic Willyama and Mt. Painter blocks. The Cambrian sediments rest unconformably on the older rocks, and, in most areas of the Adelaide geosyncline, consist essentially of three clastic sequences separated by an upper and a lower carbonate sequence (fig. 1, col. 4). The lowest clastic sequence comprises thin transgressive sandstone-siltstone units that contain faunas of Tommotian Age (Daily, 1976). This clastic sequence is overlain by a shallow marine carbonate sequence that is highly fossiliferous at some levels. Fossils include trilobites (Yorkella, Eoredlichia, ?Dolerolenus, Praraia) gastropods, hyolithids, bivalves, brachiopods, and abundant archaeocyathids. In the Adelaide area, there is a small area of andesitic volcanics near the base of the lower carbonate sequence (fig. 1, col. 3). At the end of the Early Cambrian, the red to brown micaceous shales and siltstones of the Billy Creek Formation were deposited as a shallow-water, marginal marine to paralic sequence that spread over the Adelaide geosyncline in response to tectonic uplift (Kangarooian movements) in the southern part of the basin (Moore, 1979). Thin, widespread tuff bands may have been derived from the Mt. Wright volcanic belt of the Gnalta area in western New South Wales. Trilobites in the Billy Creek Formation include Redlichia, Balcoracania and Estaingia.

The Kangarooian movements resulted in the uplift of the Yorke Peninsula area (fig. 1, col. 2), stripping some of the previously deposited Lower Cambrian sediments, and rapid deposition of fanglomerates and associated shallow-marine clastics in surrounding areas.

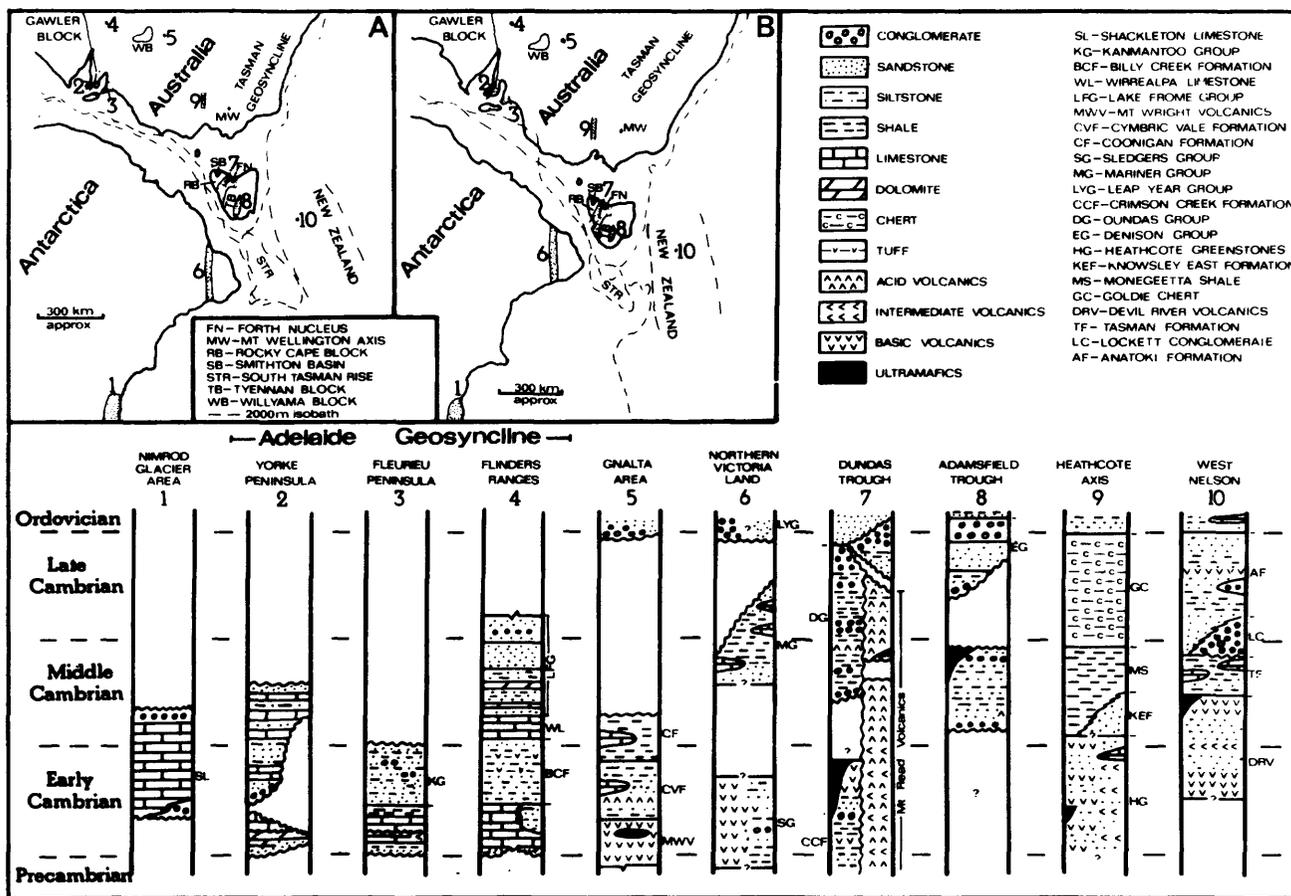


Figure 1.--Cambrian correlation chart for the southwestern Pacific part of Gondwanaland. A, Reconstruction modified from Laird and others (1977); B, reconstruction, modified from Jago (1980).

Further away from the area of uplift, there was rapid deposition of the thick, largely unfossiliferous sands and silts of the Kanmantoo Group. Some workers consider the Kanmantoo Group to be entirely of shallow-water marine origin, whereas others suggest that it is at least partly of turbidite origin.

In the main part of the Adelaide "Geosyncline" in the Flinders Ranges (fig. 1, col. 4), the Billy Creek Formation is overlain by the upper carbonate sequence, the shallow-water marine Wirrealpa Limestone, and equivalents of early Middle Cambrian age. Fossils include trilobites (*Redlichia*), archaeocyaths, sponges, and brachiopods (Youngs, 1977). The upper clastic sequence, the Lake Frome Group, is essentially a shallow-marine to nonmarine clastic sequence, which at the base is of Middle Cambrian age, but at the exposed top may be of Middle Cambrian, Late Cambrian, or even Ordovician age. Metadoxidid trilobites are known from near the base of the Lake Frome Group (Daily, 1976).

**Western New South Wales:** In western New South Wales, in the Gnalta area (fig. 1, col. 5) at what is variously regarded as the eastern edge of the Adelaide

geosyncline, the western margin of the Tasman geosyncline, or a separate depositional area are related to the Cambrian basins of central Australia, are some isolated areas of Cambrian rocks.

The oldest Cambrian rocks of western New South Wales are the spilitic, intermediate and mafic volcanics, cherts, limestones (some of which contain archaeocyaths), and shales of the Mt. Wright Volcanics. The overlying Cymbric Vale Formation (cherts, acid-intermediate tuffs, siltstones, sandstones, and limestones) contains archaeocyathids, trilobites, hyolithids, and other fossils of late Early Cambrian age (= lower Sanashtykagol horizon, Kruse, 1978). The overlying limestones and shales of the Coonigan Formation contain Ordian-Templetonian fossils including trilobites, hyolithids, sponges, brachiopods, molluscs, and some coral-like organisms (Jell and Jell, 1976; Runnegar and Jell, 1976). Upper Cambrian-Lower Ordovician conglomerates and sandstones overlie the older sediments (Webby, 1978).

## MIDDLE TO UPPER CAMBRIAN CLASTIC SEDIMENTS

Northern Victoria Land: The Bowers Supergroup contains all known lower Palaeozoic sedimentary rocks of northern Victoria Land (Laird and others, 1977). It crops out in a long (300 km), narrow (20-25 km), northwest-southeast striking strip (Bowers Trough of Laird and others, 1977). Both to the southwest and northeast the rocks of the Bowers Supergroup are in probable faulted contact with Precambrian sequences.

The Bowers Supergroup consists of three major units (Sledgers Group, Mariner Group, and Leap Year Group) separated by unconformities (Laird and others, 1981). The Sledgers Group (fig. 1, col. 6) consists of more than 3000 m of basic volcanics that interfinger to the southeast with clastic marine sediments that contain acritarchs of possible Vendian age, but also probable inarticulate brachiopods, which suggest that deposition of the Sledgers Group did not cease until at least the Early Cambrian. There appears to be a major break, representing much of the Early and Middle Cambrian, between the time of deposition of the Sledgers and Mariner Groups (Cooper and others, 1981).

The Mariner Group comprises more than 3000 m of sandstone, mudstone, and limestone forming a transgressive-regressive sequence dominated by shallow- and marginal-marine environments. Parts of the Mariner Group are richly fossiliferous, with a diverse assemblage of trilobites, brachiopods, molluscs, sponges, and trace fossils that range in age from late Middle Cambrian to middle Late Cambrian. The Mariner Group is overlain unconformably by the mainly fluvial Leap Year Group, which in one or two localities contains trace fossils indicating at least some marine influence.

Tasmania: The main area of Cambrian sedimentation in Tasmania, the Dundas Trough, is between the Precambrian Rocky Cape, Tyennan, and Forth crustal blocks (fig. 1). The axial region of the Dundas Trough (fig. 1, col. 7) contains two main marine sedimentary sequences separated by an inferred unconformity (Williams, 1978). The older sequence (Crimson Creek Formation and correlatives) consists of sandstones, mudstone, and some lithic wacke and basic volcanic horizons. A number of ultramafic and mafic complexes are associated with the older sedimentary sequence. These complexes are within the unfossiliferous mudstone of the Crimson Creek Formation, and at the structurally conformable, but erosional boundary between the Crimson Creek Formation and the younger sedimentary sequence (Dundas Group and correlatives). The Dundas Group and correlatives consist of turbidite lithic-wacke, mudstone, conglomerate and some acid volcanic layers. It contains rich, but poorly preserved fossil assemblages, that range in age from the Ptychagnostus

gibbus Zone to about the pre-Payntonian-A Stage (Jago, 1979). Around the northern and western margins of the Tyennan block, between it and the Dundas Trough, accumulated a considerable pile of acid to intermediate volcanics constituting the Mt. Read volcanic belt, that contains most of the major mineral deposits of Western Tasmania. At least in the Queenstown area, the bulk of the Mt. Read Volcanics are older than the late Middle Cambrian, but volcanism continued well into the Late Cambrian (Corbett, 1979). Both the Dundas Group and the Mt. Read Volcanics are overlain with either conformity or unconformity by terrestrial fans of siliceous conglomerate and shallow-marine conglomerate and quartz sandstone.

Other areas of Cambrian sedimentation in Tasmania include the Adamsfield Trough and the Smithton Basin (fig. 1). In the structurally complex Adamsfield Trough, (fig. 1, col. 8), there appears to be a Proterozoic sedimentary sequence unconformably overlain by a fossiliferous middle-late Middle Cambrian sedimentary sequence that, at least in one place, is intruded by an ultramafic body. Both the Middle Cambrian sediments and ultra-mafic body are overlain unconformably by the Denison Group that contains middle Late Cambrian fossils at the base, and that comprises a proximal quartz-wacke flysch at the base overlain by shallow-marine and nonmarine sediments which pass up into marine Lower Ordovician sediments (Corbett, 1975). Small amounts of acid to basic volcanics probably are associated with the lower part of the Middle Cambrian sedimentary sequence. In the Smithton Basin, there is a poorly known sequence of tholeiitic lavas, mudstones, and greywacke with well-preserved late Middle Cambrian fossils (Nepaea, Centroploera, Pianaspis, and others) at one locality.

Victoria: Fossiliferous Cambrian sediments in Victoria are known only from the Heathcote and Mt. Wellington axes, both of which are structurally complex north-south trending belts separated from surrounding lower Palaeozoic sediments by faults. In the Heathcote axis (fig. 1, col. 9) the oldest rocks are the Heathcote Greenstones comprising meta-andesite and metabasalt and associated sediments, that in two places contain Early Cambrian fossils. The Heathcote Greenstones probably extend into the Middle Cambrian; they are overlain by the Knowsley East Formation which is partly equivalent to, and partly overlain by the Monegeetta Shale. Late Middle Cambrian trilobites and a rich dendroid fauna are known from these units that are overlain by the Upper Cambrian Goldie Chert which passes up into fossiliferous Lower Ordovician sediments.

In the Mt. Wellington axis (fig. 1), similar metabasalts, volcanoclastic sediments, shales, and cherts, intruded by dolerites and ultramafics, contain late Middle to early Late Cambrian fossils.

New Zealand: All known fossiliferous Cambrian rocks in New Zealand come from the West Nelson area of the South Island, where the lower Palaeozoic rocks occur in three distinct, complex sedimentary belts separated by faults (Grindley, 1978). All known Cambrian fossils come from the Central Belt (fig. 1, col. 10), the oldest Cambrian rocks of which are probably the Lower to Middle Cambrian Devil River Volcanics comprising spilitic basic to intermediate volcanics and tuffs with subordinate volcanigenic sediments. There are overlain by the Tasman Formation which comprises siltstones, sandstone, and bands and lenses of limestone, some of which are allochthonous (Cooper, 1979). Some of the limestone contains late Middle Cambrian trilobites and brachiopods. The Tasman Formation is overlain by the polymict, largely nonmarine Lockett Conglomerate that is largely derived from older Cambrian formations. Partly equivalent to, and partly overlying the Lockett Conglomerate, are the volcanoclastic sandstone and siltstone, volcanic flows and sills of the Anatoki Formation, a possible equivalent of which from an isolated area, contains the only known Late Cambrian fossils in New Zealand (Cooper, 1979). The Cambrian rocks are overlain conformably by fossiliferous sediments of Tremadocian age.

This work was supported by the Australian Research Grants Committee. Some of the stratigraphic columns shown in figure 1 result from the writer's participation in I.G.C.P. Project 7, "South-west Pacific Basement Correlations".

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## 28. TRENDS AND PROBLEMS IN CAMBRIAN TRILOBITE EVOLUTION

By

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A phylogenetic classification of Cambrian trilobites based on a small number of "key" characters is now dismissed by most researchers. Elucidation of details of individual lineages must lead to phylogenies. Recently, attempts have been made to place identifiable taxa of different levels into categories, based on the biofacies in which they occur. Such divisions have not attempted to include any biological features, but have assumed that some trilobites possess features that restrict their taxon to a particular biofacies. Many living crustacean groups are not so restricted.

By analogy with living crustacean taxa, a variety of feeding habits are inferred to have existed in the Trilobita, represented by different appendages and different specializations of the anterior of the alimentary canal. The latter specializations in trilobites may be expressed in the shape of the glabella, because the relatively flat trilobite body probably could not accommodate evolution of major food processing apparatus without concomitant alteration of the exoskeleton.

An examination of Cambrian trilobites shows that the typical ptychoparioid morphology (anteriorly tapering convex glabella not reaching border furrow, 10-15 thoracic segments, transverse small pygidium) is prevalent throughout the Cambrian and could have been an unbroken lineage. Although unlikely to have been the original or "most primitive" trilobite morphology, the ptychoparioid morphology may have filled an unoccupied niche and was not displaced for a long time. Each other morphological type may have evolved from a ptychoparioid morphological type once or on several occasions. In most cases, offshoots from this typical morphology appear to have become specialized in some way and then became extinct lineages or continued in the same trend from a less specialized member of the offshoot. Several major

morphologies are:

1. Redlichioid (glabella reaching border furrow, narrow, tapering, convex; pygidium small; more than 15 thoracic segments).
2. Dorypygid (glabella bulbous, laterally expanded, reaching anterior border furrow; large pygidium often spinose; fewer than 10 thoracic segments).
3. Catillicephalid (glabella very large bulbous occupying most of cephalon; small pygidium; small number of thoracic segments).
4. Damesellid (narrow, convex glabella reaching anterior border furrow; large, usually spinose pygidium; 10-15 thoracic segments).
5. Menomoniid (short glabella, but with preglabellar boss; small pygidium, many thoracic segments).
6. Paradoxidid (large anteriorly expanded, but relatively low glabella reaching anterior border furrow; either large spinose pygidium and few segments, or many segments and small pygidium).
7. agnostoid (2 or 3 thoracic segments; isopygous; glabella short, not reaching anterior border furrow).

Not all species will fit these criteria exactly, but may be intermediate in one or more characters between the ptychoparioid morphology and any one of these morphs. Each of these morphs may not indicate a different feeding type, but an attempt is made to interpret each of these glabellae in terms of feeding mechanism. In this way, we may come to better understand the variety within a larger taxon and the limitations of the inferences from biofacies associations. Generalizations on biofacies indications from taxonomic groups should take into account within-group variation in feeding habit if possible.

Stage	China		Australia		Canada	U.S.A.	Sweden	Norway	U.S.S.R.		
Meishucun Stage	Yunnan	Meishucun	Sichuan Maidiping	South Australia Flinders Ranges (Daily, 1972)	Central Australia Amadasi Basin (composite)	Southern Cordillera (Young, 1971)	California (composite)	(composite)	(composite)	Russian Platform	Siberian Platform
	Badawon Member	[S.4] <i>Plagiogmus arcuatus</i> <i>Gordia moendina</i>  Worm trail form A	Jiulaodong Fm. <i>Plagiogmus</i>	<i>Plagiogmus</i>	Member <i>Gordia</i> <i>Rouaultia</i>	McNaughton Fm. <i>Scolithos</i> <i>Cruziana</i> <i>Rusophycus</i> <i>Diplichnites</i>	Middle-Upper Member <i>Monocraterion</i> <i>Scalicia</i> <i>Diplichnites</i> <i>Rusophycus</i> <i>Plagiogmus</i> ? (= <i>Pteridinium</i> )	Norretorp Sandstone	Holma Series	Baltic Series	Tomtoian Stage
	Zhongyicun Member	[S.3] <i>Didymaulichnus mieltensis</i> <i>Rusophycus</i> sp  [S.2] <i>Cavaulichnus viatorus</i>	Maidiping Fm.	<i>Phycodes pedum</i> <i>Rusophycus</i> and other trace fossils	Arumbera Fm. Member <i>Diplichnites</i> Molluscan trails B-D (= <i>Didymaulichnus mieltensis</i> ) <i>Phycodes pedum</i> <i>Rusophycus</i> -like	Upper Miette Unit <i>Didymaulichnus mieltensis</i>	Deep Spring Fm. <i>Rusophycus</i>	Diplocraterion <i>Syrngomorpha</i>	Diplocraterion Monocraterion Skolithos	Cochlichnus <i>Treptichnus triptex</i>	Chondrites <i>Planolites</i> <i>Rhizocorellium</i>
	Xiaowatoushan Member	[S.1] <i>Salleulichnus meishucunensis</i>	Maidiping Fm.	Uratama Fm.	I Member		Lower Member <i>Wyattia</i>	Hardeberga Quartzite <i>Rusophycus</i>	Mjisa Quartzose Sandstone	<i>Harlanella podolica</i> <i>Paleopascichnus delicatus</i>	
						Reed Dolomite		Ekra Shale	Vendian Series	Yudomian Fm. <i>Planolites</i> <i>Cochlichnus</i> <i>Berganeria</i>	

Figure 2.--Proposed correlation of the Meishucun Stage of China with strata worldwide considered to be lowest Cambrian in this report.

principle of determining the beginning of Cambrian according to the earliest occurrence of small shelly fossil assemblages. However, biological evolution is continuous, and the observed occurrence of the earliest assemblage only represents our knowledge at present and the degree to which our present research can obtain.

Widely distributed trace fossils have been found within the strata of the Meishucun Stage. A succession of four forms has wide significance for correlation (fig. 1). The forms probably belong to the *Skolithos* and *Cruziana* facies. Only in the Meishucun Stage have these trace fossils (*Didymaulichnus* and *Plagiogmus*) been found with small shelly fossils. These occurrences are therefore most significant for studies of the Precambrian-Cambrian boundary.

Mainly on the basis of research achievements in small shelly and trace fossils, but also as a result of isotopic age determinations, paleomagnetic stratigraphy, and lithostratigraphy, it is suggested that the boundary between the Precambrian and Cambrian should be placed at the base of the Meishucun Stage.

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### 30. EXAMPLES OF CAMBRIAN MINERAL DEPOSITS

By

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Stratiform and stratabound mineral deposits associated with particular Cambrian facies are known the world over. This summary is a sampling of the types of mineral deposits known to occur in Cambrian rocks. To a degree, this effort should make stratigrapher-sedimentologists and economic geologists more aware of the mineral potential in these lower Paleozoic rocks and cognizant of facies relationships useful as exploration guides.

Carbonate-hosted Mississippi Valley type lead-zinc deposits of Cambrian age have been extensively studied in the United States and Canada. Host rocks include the Upper Cambrian Bonnetterre Formation in Missouri (Grundmann, 1977; Sweeney and others, 1977); the Lower Cambrian Sekwi Formation of the Mackenzie Platform in the Northwest Territories, Canada (Brock, 1976; Smith, 1974); and the Middle Cambrian to Lower Ordovician(?) Metaline Limestone in northwestern Washington (Park and Cannon, 1943). These deposits are epigenetic in that the sulfides were deposited in open-space structures of various origins formed in platform carbonates. Unconformities above and sometimes below the carbonate host, dolomitization, karst and (or) evaporite-solution breccia structures, and nearby shale basins (as a potential source of metalliferous brines and sulfide) are common associates.

Beds containing galena, sphalerite, and copper sulfide laminae interbedded with shales and (or) sandstones, and in some instances pyroclastics and felsic lavas, are also well known. The origin of some of these deposits in terms of timing (syngenetic, diagenetic, and (or) epigenetic) and the source of the ore fluids (volcanic-exhalative or strictly sedimentary) are controversial. Several of these deposits have been metamorphosed, making genetic interpretations more difficult. Shale-hosted lead-zinc sulfides occur in Cambrian and Cambrian-Ordovician rocks of the Selwyn Basin, Northwest Territories, Canada. Stratiform copper sulfides that include volcanic units are known from the Mindaman Mine, Nova Scotia (Watson, 1954); the Ascot Mine, Quebec, Canada; and at Mt. Lyell and Rosebery in south Australia (Reid, 1975; Markham, 1968; Burton, 1975). Copper deposits also occur in Cambrian red beds in the Lena River area of Russia (Nalivkin, 1973). Low-temperature metalliferous brines are believed to be the source of

the lead-zinc mineralization in shallow-water platform sandstones of the Lower Cambrian Laisvall Sandstone of Sweden (Rickard and others, 1979).

A variety of industrial minerals of Cambrian age are of economic value. Limestone, dolomite, and phosphorites are the most important deposits. The latter are known chiefly from Australia, China, Vietnam, and Russia, but phosphorites are recognized in Tennessee and Canada as well (Cook and McElhinny, 1979). Cambrian phosphorites are largely of the pelletal type that accumulated on low- and middle-latitude continental shelves. Of minor economic importance are bedded magnesite in the Lower Cambrian of the Purcell Mountains, British Columbia (Douglas, 1970); rock salt (Lower Cambrian, Lena River area, Russia); manganese (Middle Cambrian, Russia, and Newfoundland); and potassium, derived from alunite nodules in a Cambrian shale in Australia (Johns, 1976).

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# 31. RAMP AND PLATFORM DEPOSITION DURING THE MIDDLE CAMBRIAN, EASTERN CALIFORNIA AND WESTERN NEVADA

By

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The structure of the Middle Cambrian shelf in eastern California and adjacent Nevada seems to have taken the form of a ramp in the early part of the epoch and then, possibly as a consequence of syndepositional faulting, that of a platform toward the end of the Middle Cambrian (Kepper, 1981). One of the critical sections in this interpretation is at HorseThief Canyon, California (H on fig. 1) where a shelf-carbonate lithosome is inferred to intertongue with a basin lithosome. Basin, as used here, refers either to the deeper water environments on distal portions of a ramp or to seaward of a platform. Stratigraphic units involved in this reconstruction include from the Last Chance Range (13 km south of Horse Thief Canyon), the Bonanza King Formation consisting of the Papoose Lake Member and the overlying Banded Mountain Member, and the Emigrant Formation in California and Nevada. The Emigrant is subdivided into four members at Horse Thief Canyon represented by a basal limestone-siltstone member, a dolostone member, a megabreccia member, and a limestone-chert member. Stratigraphic relationships between sections in California and Nevada (fig. 2) are based on a combination of biostratigraphic and lithostratigraphic interpretations that are more fully discussed in Kepper (1981).

There are four prominent lithologic types in the Bonanza King of the Last Chance Range. These types include: black, thin to thickly bedded pelletal dolostone; light- to medium-gray, thick- to medium-bedded, laminated intraclastic-pelletal dolostone; tubular burrowed to mottled dolostone; and rust-colored dolomite siltstone to very fine grained sandstone. The Papoose Lake Member is dominated by massive black pelletal dolostone. A distinctive rust-colored siltstone marks the base of the Banded Mountain Member which here is differentiated from the lower member by a higher frequency of bands, by thinner bands of light and dark dolostone, and by the presence of thin rusty siltstones in at least the lower third of the member. Simple A-B type cycles make up both the top of the Papoose Lake and much of the Banded Mountain. These cycles consist of an upper unit of tubular burrowed to mottled dolostone and a lower unit of laminated dolostone that occasionally shows ripple and flaser structures. The bioturbated unit makes sharp contact with the underlying bedded

dolostone, and burrowing does not appear to cross this boundary. Burrowing is generally weakly developed in the lower part of the unit. The upper contact of the burrowed unit is more irregular, showing some evidence of truncation by bottom currents before the overlying laminated unit was deposited.

Mottled and tubular burrowed dolostone contain bioturbation structures indicative of extensive reworking of the carbonate muds by sediment-feeding organisms. The rhythmic alternation of bedded and bioturbated dolostones indicates that periods of lower current strength, little sediment input, and combined with intense biologic reworking of bottom sands and muds were terminated by periods of stronger currents and higher influx of sediments not conducive to

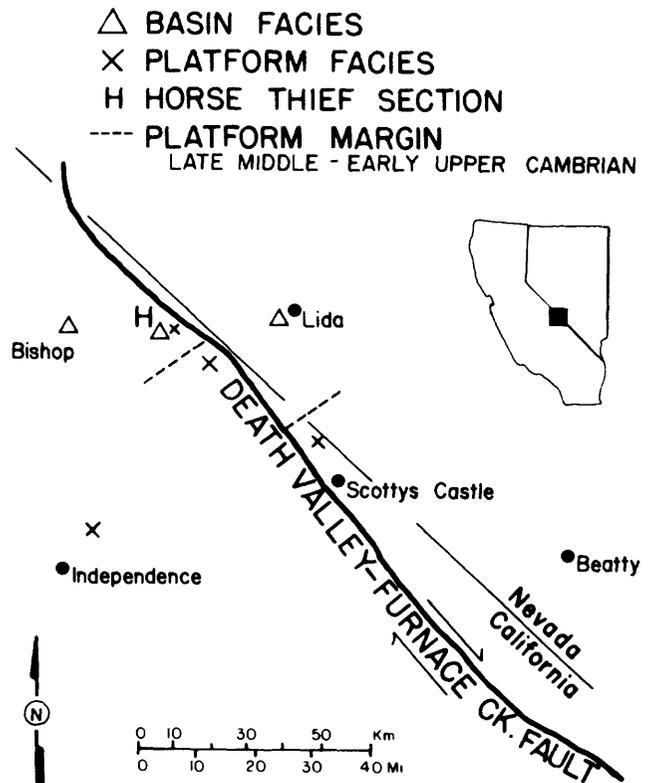


Figure 1.--Index map of study area showing major structural features.

organic activity. Scattered intraclastic layers probably were produced in induration and (or) cementation of surface layers that were later disturbed by burrowing organisms and reworked by bottom currents.

Bedded and mottled dolostones similar to those in the Last Chance Range occur farther south in the Grapevine Mountains and in the Bare Mountains near Beatty, Nev. These banded dolostones were part of a blanket of sediment deposited on the ramp seaward of a zone characterized by shallow subtidal and peritidal conditions (Kepper, 1976, p. 77). Peritidal environments alternating with subtidal conditions are the major cause for the rhythmic banding typical of the Bonanza King in the more easterly sections. The occurrence of banding of different origins over approximately the same stratigraphic interval suggests a causal relationship. Mud production may have corresponded with shallow subtidal conditions on midshelf, while biogenic reworking of sediments was occurring farther out on the ramp. Onset of peritidal conditions led to the redistribution of midshelf sediments and an increase in the intensity of bottom currents, as evidenced by units of bedded dolostone farther out on the shelf. A more fundamental cause is probably related to shifting current patterns controlled by the extent of peritidal shoals midshelf.

The megabreccia member is in depositional contact with a tongue of the Papoose Lake Member, and is characterized by megabreccia (clasts greater than 1 m) and breccia (clasts less than 1 m) beds interbedded with allodapic carbonates, including pebbly calcarenite, calcarenite and calcisiltite units. This abrupt shift to a very coarse clastic texture indicates that the older ramp structure was modified to a platform with a distinct break in slope between shelf and basin depositional sites. Megabreccia beds seem to be confined to the lower part of the member where the thickness of individual beds is as much as 15 m. Pebbly calcarenites grade upward from breccia beds interbedded with allodapic intervals. Some calcarenites form lenses representing either channel structures or fillings of depression on the upper surface of megabreccias. Calcarenite and calcisiltites generally form very thin to thin interbeds with an even to lenticular (rippled) bed form in intervals ranging in thickness from a few meters to tens of meters.

Megabreccia beds contain clasts as much as 6 m across in a mud-supported framework. Platy black calcisiltite clasts make up 65 percent of the rock types, and gray calcarenite and light-gray algal boundstone (with well-preserved *Epiphyton* structures) represent the remaining 35 percent. The matrix is a sandy mud containing pellets, sand-size clasts, and rarely oolites and trilobite fragments. Clasts in breccia beds and some megabreccias commonly show a subhorizontal fabric. Inclined clast fabric, particularly the waveform clastic fabric in which the inclinations

of clasts are in opposite directions along the same bed (Hubert and others, 1977, p. 133) occur in a few megabreccias at Horse Thief Canyon. Absence of other directional structures, in addition to structural complications, preclude determining the direction of movement. In the thicker megabreccia beds, large clasts locally have vertical orientations. Some allodapic beds contain sand- and silt-size pellets and clasts in a mud matrix. Contacts are sharp between beds and no grading was observed. No bioturbation structures were noted in the allodapic units.

The megabreccias are believed to be submarine debris-flow deposits derived from a nearby platform margin. Evidence for high viscosity flows includes: clasts projecting above the top surface of the beds, large elongate clasts oriented at a high angle to bedding, waveform-inclined clast fabric, matrix-support fabric, and poor sorting (Harms, 1974, p. 1778, Hubert and others, 1977, p. 139). Lower viscosity flows have subhorizontal fabric. Pebbly calcarenites and calcarenite associated with megabreccias and breccias represent either late surges associated with the main flow or distal equivalents of separate debris flows.

Algal boundstone clasts are similar to light-gray, recrystallized fenestral limestones near the base of the Papoose Lake Member and in the upper Carrara Formation in the Northern Last Chance Range. This rock type is not present higher in the Middle and Upper Cambrian section here. Platy calcisiltite clasts may largely be reworked from the apron of sediment developed at the base of the platform, but some may have come from the peloidal carbonates on the platform itself. Grains in the allodapic beds represent sediment periodically washed off the platform or resuspended from the apron of sediment building up at the base of the slope. Absence of biogenic activity in the apron sediment suggests that the pellet material probably came from the platform where the pelletal sediments dominated.

To generate these debris flows, a slope must have formed during the Middle Cambrian. There are at least three possibilities regarding the formation of such a slope. The first is that an algal buildup, as described by McIlreath (1977, p. 115) from the Cambrian of western Canada, developed on the outer ramp and made it into a platform. Except for a few thin units of fenestral carbonate in the upper Carrara and basal Bonanza King (fig. 2), no such buildup is evidenced in the present North Last Chance Range sections. Possibly, the Horsethief Canyon section could be in thrust relationship to the North Last Chance Range (although the thrust would now be below the surface) covering an outer platform algal boundstone interval. Alternatively, the lithologic similarity between the tongue of the Papoose Lake and the Papoose Lake Member (both are thinly bedded peloidal dolostones) suggests that they may have been

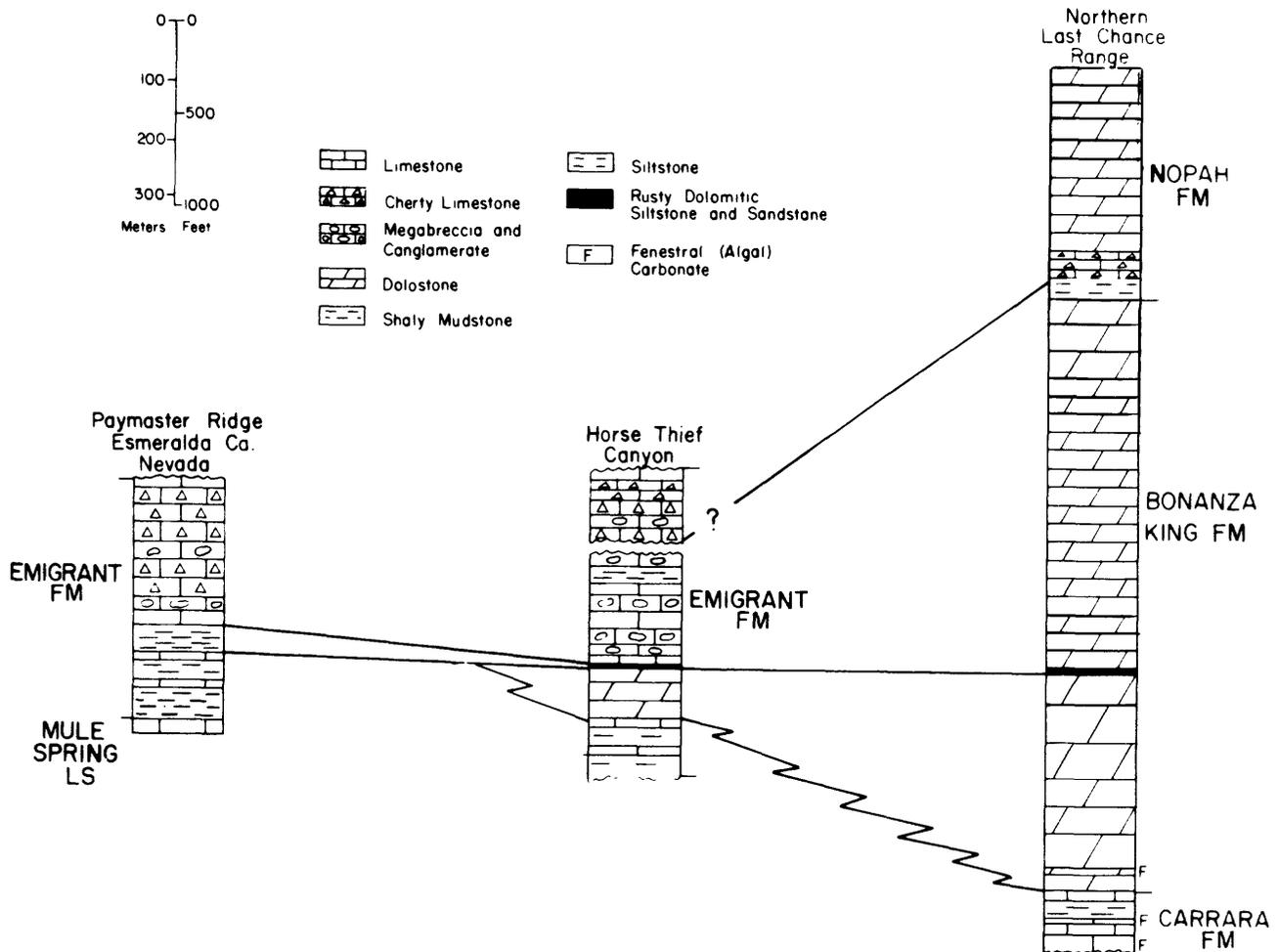


Figure 2.--Diagram showing platform margin-basin stratigraphic correlations.

deposited in proximity to one another, and that no buildup lay between them.

A second possibility is that there was never a significant organic buildup, merely scattered algal mounds on the ramp as represented by the fenestral carbonates in the lower Bonanza King and underlying Carrara Formations. Increase in slope as a consequence of tilting or differential subsidence led to a slope along which debris flows formed. It is difficult however to visualize, considering the thickness and lateral extent of the breccia, such deposits forming from localized sources. Further, the stratigraphic position of known sources is well below (2000-3000 ft or 620-915 m) a rusty dolomitic siltstone marker at the base of the Banded Mountain Member in the Northern Last Chance Range (fig. 2). This marker is equated with the rusty siltstone that is below the megabreccias at Horse Thief Canyon. In other words, the postulated source is much older than, not contemporaneous with, the debris-flow deposits.

This stratigraphic relationship leaves open a third possibility, namely that part of the ramp collapsed during the Middle Cambrian exposing the fenestral carbonates (algal boundstone) lower down in the Cambrian section. There is no evidence of uplift and emergence of the ramp, so collapse is the more likely process. This postulated Middle Cambrian syndepositional fault could be related to other Cambrian platform configurations to the north in Nevada, or, alternatively, to an easterly trending structure bounding the south side of the House embayment (Kepper, 1981). Such east-west oriented Paleozoic structures as the House embayment of the Cortez-Uinta High of Roberts (1968, p. 105) may be guided by older Precambrian structures transverse to the trend of the Cordilleran geosyncline (Burchfiel and David, 1975).

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## 32. CAMBRIAN FAUNAS IN THE LIMESTONE CONGLOMERATES OF WESTERN NEWFOUNDLAND

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Sporadic outcrops of limestone conglomerates interbedded with shale and thin-bedded limestone constitute the Cow Head Conglomerates of the west coast of Newfoundland (fig. 1). Some boulders in these conglomerates contain well-preserved trilobites. Professor H. B. Whittington and I (Kindle and Whittington, 1958) have found that the trilobites in almost all boulders from any one of these conglomerates are commonly of the same age, although individual conglomerate beds range in age from Middle Cambrian to Middle Ordovician.

This report was first read in September 1978 at the Corner Brook, Newfoundland, meeting of the Eastern Paleontology and Biostratigraphy Seminar. Subsequently, the Cambrian collections discussed here became the property of the Geological Survey of Canada and are now housed in Ottawa. This report is intended as a summary of preliminary identifications of trilobite taxa associated with individual numbered boulders in various units of the Cow Head Conglomerates. A classification of the the boulders into faunal zones and an age interpretation for each faunal zone are suggested.

### ZONE 1

In the Broom Point area (fig. 2), Sandy Cove has an anticlinal structure. At the water's edge on both sides of this cove is the oldest conglomerate unit in the Cow Head Conglomerates. Boulders 358, 362, and 380 from this unit yielded Bathyriscus adaeus, Peronopsis with a deep transverse furrow on the posterior lobe of the pygidium, Zacanthoides with slender upturned pygidial spines, strongly pustulose Chancia, Tonkinella and Oryctocephalus. Other boulders in this and the overlying 4-foot (1.2 m) conglomerate, which are separated by gray limestone beds, yielded Pagetia, Peronopsis, Ptychagnostus cf. P. gibbus, Kootenia, Elrathia, and Onchocephalites.

### ZONE 2

In addition, the 4-foot conglomerate (some labels read "5-foot") has yielded Baltagnostus, Zacanthoides with 6 pairs of pygidial spines, and rare specimens of

Centropleura (a cephalon in deep-water limestone), here assigned to Zone 2. Zones 1 and 2 are correlated with the Bathyriscus-Elrathina Zone of the Rocky Mountains (Rasetti, 1951) and with Zone B1 of the Middle Cambrian of Sweden (Westergård, 1946).

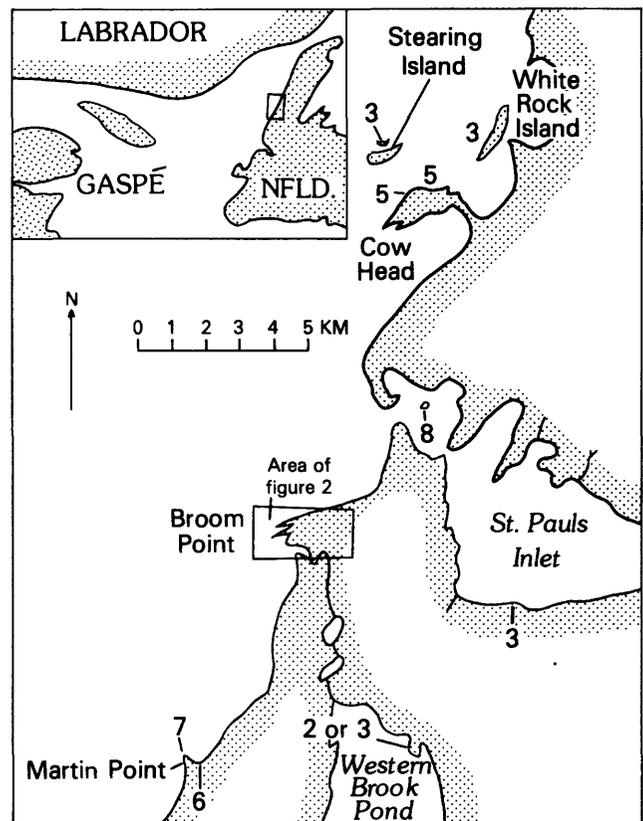


Figure 1.-- Map of the Cow Head-Broom Point area, western Newfoundland, showing locations of some outcrops representing certain faunal zones (marked by appropriate numbers).

Outcrop areas not shown here include Green Point (Zone 8), 13 km south of the map area; and Bear Cove (Zone 7) and Serpentine River (Zone 8), both about 120 km south.

### ZONE 3

In white limestone beds overlying the 4-foot conglomerate, and in some white limestone boulders in the overlying 50-foot (15-m) conglomerate on the south shore of Sandy Cove (fig. 2) and at other localities shown on figure 1, younger Middle Cambrian faunas assigned to Zone 3 are found:

Boulder 448 (white limestone beds)--Tomagnostus fissus, Hypagnostus parvifrons, ?Ptychagnostus atavus, ?Cotalagnostus, Meneviella venulosa, ?Alokistocare.

Boulder 450 (50-foot cgl.)--Peronopsis, Tomagnostus, Meneviella venulosa, Bailiaspis.

Boulder 452 (50-foot cgl.)--Eodiscus, ?Hypagnostus, Ptychagnostus atavus, Tomagnostus, Alokistocare, Spencella.

Boulder 632 (White Rock Islets)--Tomagnostus fissus, Hypagnostus, Peronopsis, Bailiaspis, ?Sclenopleura, ?Elrathia, Centropleura (pygidium).

Boulder 603 (White Rock Islets)--Kingstonioides (2 sp.), Bolaspidella, Catillicephalites, Alokistocare, Orria, Olenoides (large strong spines), Modocia, Elrathia, Spencella, ?Bathyriscidella, ?Corynexochides.

Boulder 619 (White Rock Islets)--Ptychagnostus atavus, Hypagnostus parvifrons, Peronopsis, Bathyriscus, Olenoides (like in 603).

Some of these trilobites have also been seen at White Point in St. Pauls Inlet, at Eastern Point in Western Brook Pond, and in the outer reefs of Stearing Island (fig. 1). Zone 3 is correlated with Zones B2 and B3 of the Middle Cambrian of Sweden (Westergård, 1946).

### ZONE 4

Above Zone 3 south of Sandy Cove, a unit of dark shale has yielded no fossils. However, above this shale is the 50-foot conglomerate in which most fossiliferous boulders have trilobites younger than those of Zone 3. They are:

Boulder 458--Ptychagnostus aculeatus, Phalacroma glandiforme, Lecanopleura, ?Bynumia, Onchonotopsis (with occipital spine).

Boulder 466--Hemirhodon, Blountia.

Boulder 468--Phalacroma glandiforme, ?Bynumia, Blountia (punctate), ?Bolaspis (anterior spine), ?Lonchocephalus, n. gen. (flat neck merges with cheeks), small cephalon with pitted surface.

Boulder 470--Kormagnostus, ?Homagnostus, Hemirhodon, ?Bolaspis (swollen brim and flat neck spine), Arapahoia, ?Aposolenopleura.

Boulder 469--Bolaspidella, Bolaspis (anterior extension), ?Liostracionoides (pitted with some pustules).

Boulder 472--n. gen. (aff. Dartonaspis), ?Liostracionoides (pitted surface).

The presence of Ptychagnostus aculeatus and Phalacroma glandiforme shows that Zone 4 correlates with Zone C2 of the Middle Cambrian of Sweden (Westergård, 1946). Boulders with faunas of this zone have not been found at any other localities. Above the 50-foot conglomerate in the Broom Point area, no fossiliferous boulders have been seen north of the vicinity of Western Brook, where boulders from Zone 8 have been identified. On the north side of Sandy Cove above Zone 1, boulders which are labelled "equivalent to the 50-foot conglomerate" yield faunas of Zone 7. The stratigraphically higher conglomerate next to Mudge Cove contains boulders with faunas of Zone 8.

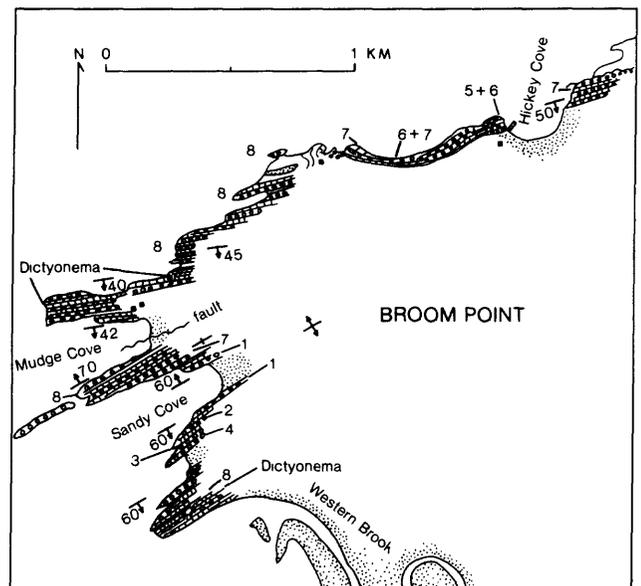


Figure 2.--Broom Point area, showing Cambrian faunal zones (numbers 1 to 8 on map). Patterned area represents outcrops of the fossiliferous Cow Head Conglomerates. Oxley (1953) was the first to find fossils in this area, both in Zone 3 and at low tide in the bed of Western Brook. These Ordovician trilobites were described by Rasetti (1954). The conglomerate between Zone 3 and the small Dictyonema-bearing hill near the mouth of Western Brook has yielded specimens of Hystricurus, Yukonaspis, and Boeckaspis hirsuta, which are now part of the Geological Survey of Canada's collection in Ottawa. The latter species is known from the early Tremadocian of Norway (Henningsmoen, 1957).

ZONE 5

Boulders with trilobites of Zone 5 have been collected on the north shore of Cow Head. *Pseudagnostus* is common in this and following zones and is omitted in the lists.

Boulder 11--*Clavagnostus*, ?*Baltagnostus*, *Cedaria*, *Crepicephalus*, *Tricrepicephalus*, ?*Meteoraspis*, *Kingstonia*, *Holcacephalus*, *Blountia*, *Onchonotopsis*, ?*Bolaspidella*, ?*Liostracinoidea*.

Boulder 34--*Clavagnostus*, new agnostid, *Cedaria*, *Meteoraspis*, *Deiracephalus unicornis*, ?*Coosella*, ?*Coosia*.

Boulder 15--*Cedaria*, *Crepicephalus*, *Kingstonia*, *Deiracephalus*, *Holcacephalus*, *Terranovella obscura*.

Boulder 39--*Acmarhachis*, *Kormagnostus*, *Pseudagnostina*, *Hypagnostus*, *Aspidagnostus*, *Cedaria*, *Meteoraspis*, ?*Crepicephalus*, *Blountia*, *Holcacephalus*, *Deiracephalus unicornis*, ?*Kingstonia*, ?*Lecanopleura*.

Boulders with the Zone 5 fauna are mixed with a younger set of boulders about 1.2 km east of Broom Point (fig. 2). The conglomerate with these mixed boulders lies below a more rapidly weathering conglomerate that has Zone 7 fossils. The Zone 5 fauna is also known from Murphy Creek on the Gaspe Peninsula of Quebec (Kindle, 1948) where cephalala and pygidia of *Clavagnostus sulcatus* also occur. This species permits correlation of Zone 5 with Zone C3 of the Middle Cambrian of Sweden (Westergård, 1946).

ZONE 6

In front of the lighthouse on Cow Head, and at Broom Point and Martin Point above the conglomerate with faunas of Zone 5, there are boulders with a different fauna:

Boulder 48--*Aphelaspis*, *Blountia*.

Boulder 49--*Pseudagnostus communis*, *Aagnostus inexpectans*, *Aagnostus cf. pisiformis*, *Homagnostus cf. obesus*, *Aphelaspis*, *Dytremacephalus*, *Dunderbergia*, ?*Onchopeltis*.

Boulder 51--*Aphelaspis*, *Dytremacephalus*, *Tholifrons*.

Boulder 56--*Aphelaspis*, *Glyptagnostus reticulatus*.

Boulder 57--*Acmarhachis*, *Homagnostus cf. obesus*, *Bathyholcus*, (2 sp.), ?*Bellaspis*.

Boulder 166 (1 km east of Broom Point)--*Onchopeltis*, *Dunderbergia*, *Dytremacephalus*, *Pterocephalops*.

Boulder 528 (oldest at Martin Point)--*Aphelaspis*, *Dunderbergia*, *Dytremacephalus*, *Pterocephalops*.

In addition, the White Rocks, which are small limestone conglomerate islands in Bear Cove, 6 miles north of the Serpentine River, have boulders with a similar fauna. The presence of *Glyptagnostus reticulatus* in the Zone 6 boulders permits correlation of this Zone with Zone 2 of the Upper Cambrian of Sweden (Westergård, 1947).

ZONE 7

Boulders with faunas of Zone 7 have been found

Table 1.--Correlation of Upper and Middle Cambrian zones of western Newfoundland with those of Sweden and Norway, based on trilobites common to both areas

Sweden and Norway	Common taxa	Western Newfoundland
Lower Tremadocian-----	<i>Boeckaspis hirsuta</i> , <i>Dictyonema</i> ----	Ordovician.
Westergård's Upper Cambrian Zones		
6. <i>Acerocare</i> , + -----		
5. <i>Peltura</i> , <i>Ctenopyge</i> , + ----	<i>Peltura</i> , <i>Lotagnostus</i> -----	Zone 8.
4. <i>Leptoplastus</i> , <i>Eurycare</i> ----		
3. <i>Protopeltura</i> , + -----	<i>Protopeltura</i> -----	Zone 7.
2. <i>Olenus</i> -----	<i>Glyptagnostus reticulatus</i> -----	Zone 6.
1. <i>Aagnostus pisiformis</i> -----	<i>Aagnostus cf. pisiformis</i> -----	
Westergård's Middle Cambrian Zones		
C3. <i>Lejopyge laevigata</i> -----	<i>Clavagnostus sulcatus</i> -----	Zone 5.
C2. <i>Solenopleura brachymetopa</i>	<i>Ptychagnostus aculeatus</i> , <i>Phalacroma glandiforme</i> .	Zone 4.
C1. <i>Ptychagnostus lundgreni</i> , +		
B4. <i>Ptychagnostus punctuosus</i>		
B3. <i>Hypagnostus parvifrons</i> ----	<i>Hypagnostus parvifrons</i> -----	
B2. <i>Tomagnostus fissus</i> ,	<i>Ptychagnostus atavus</i> , <i>Tomagnostus fissus</i> , <i>Eodiscus punctatus scanicus</i> .	Zone 3.
<i>Ptychagnostus atavus</i> .		
B1. <i>Ptychagnostus gibbus</i> -----	<i>Ptychagnostus cf. gibbus</i> -----	Zones 1 & 2.

in the readily weathering conglomerate 1 km east of Broom Point, in the area north of Sandy Cove, and at Martin Point. One of the commoner trilobites in this zone is Levisella brevifrons.

Boulder 168--Homagnostus, Irvingella, Bathyholcus, Oligometopus, Xenocheilus, Richardsonella.

Boulder 172--Loganopeltoides, Taenicephalina, Phoreotropis.

Boulder 176--Parabolina cf. lobata lobata, Protopeltura?, cf. Ctenopyge (glabella too wide).

Boulder 177--Protopeltura, Levisella brevifrons, Resseraspis, Liostracinoidea.

Boulder 211--Peratagnostus, Elvinia.

Boulder 555 (Martin Point)--Levisella brevifrons, Hungaiia cf. burlingi, Simulolenus, Liostracinoidea sp., Loganopeltoides kindlei.

Boulder 554 (highest conglomerate at Martin Point)--Bathyholcus, Quebecaspis cf. coniformis, Richardsonella, Tholifrons, Xenocheilus, Oligometopus, cf. Xenocheilus.

Parabolina lobata lobata and Protopeltura occur in the lower part of Zone 5 of the Upper Cambrian of Sweden (Westergård, 1946). Peratagnostus was described by Opik (1967) from the Idamean Stage of Australia. It and Hungaiia burlingi were found by Palmer in the Franconian of east-central Alaska (Palmer, 1968).

#### ZONE 8

Boulders with Zone 8 trilobites are found in the conglomerates northwest of the small Dictyonema-bearing hill at the mouth of Western Brook, on the south side of Mudge Cove at Broom Point, below Dictyonema east of Broom Point, at Green Island in the entrance to St. Pauls Inlet, in limestone beds south of the Serpentine River, and in separate areas on Cow Head.

#### ZONE 8A

A boulder in a thick sandstone bed in front of the lighthouse on Cow Head produced Pseudosaukia brevifrons, Rasettia capax, Rasettia marcouri, Keithiella, Onchonotus globosus, Glyptomtopus laflammei, Heterocaryon, Levisella brevifrons.

#### ZONE 8B

Boulders with a fauna probably somewhat younger than that of zone 8A are found at the top of the cliff northeast of the lighthouse on Cow Head, midway between the lighthouse and a sheep trail to the shore. Blocks of rock separating from the cliff at this

point had boulders which produced Hungaiia quadrispinosa, Bienvillea, Peltura, Richardsonella, Loganellus, Loganopeltoides, Keithia, Raymondina, Onchonotus, Keithiella, Stenopilus, and Apatokephaloides.

#### ZONE 8C

Southwest of the lighthouse at Cow Head, blocks fallen from the cliff have provided boulders with Hungaiia magnifica. These must be younger than Zone 8B because, in addition to Keithia, Keithiella, Bienvillea, Loganopeltoides, and Apatokephaloides, the genera present include Corbinia (?=Bayfieldia), Yukonaspis and a new genus with a high thin ridge connecting the eyes across the glabella. Corbinia and Yukonaspis also occur in conglomerates below Dictyonema at Broom Point and near the mouth of Western Brook. On the south side of Mudge Cove, a boulder with this fauna also yielded a cephalon of Lotagnostus.

Boulder 245 (5th conglomerate below Dictyonema east of Broom Point) provided a large fauna: Pseudagnostus gyps, Pseudagnostus canadensis, Litagnostus n. sp., Corbinia, Yukonaspis, Bienvillea, Onchonotus, Loganopeltoides, Aposolenopleura, Heterocaryon, Keithia, Keithiella, Westonaspis, Leiocoryphe, Idiomesus (2 sp.), Phoreotropis, Talbotina, Apatokephalus, Apatokephaloides, Ambonolium, Euptychaspis, Plethometopus, Glyptomtopus, Stenopilus, n. gen. cf. Zacompsus (with elevated eye ridges and crest on glabella).

Boulder 493 (west of the Dictyonema-bearing hill near the mouth of Western Brook)--Prosaukia or Saukiella, Yukonaspis, Euptychaspis, Heterocaryon, Stenopilus, Leiocoryphe, Idiomesus, Theodenisia gibba, new agnostid.

From examination of these faunal lists it seems that many genera extend in time beyond where they are expected to occur. Thus, I could not place many of the boulders in any secure niche in the Dresbachian, Franconian, or Trempealeuan. All I have done is to arrange them in what seems to be their proper stratigraphic sequence. Later workers may subdivide these and make more accurate correlations.

I am grateful to Dr. H. B. Whittington for help in making the collections. For help in naming some of the bewildering array of strange trilobites, I am indebted to the late Professor B. F. Howell.

Dr. A. A. Opik, Dr. A. R. Palmer, and Dr. W. H. Fritz were also very helpful.

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### 33. ONTOGENY OF EHMANIELLA:—IMPLICATIONS FOR TRILOBITE ECOLOGY

By

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The value of ontogenetic data to the study of systematics and evolution in trilobites has long been appreciated. Whittington (1957), Palmer (1958), Robison (1967), and others have applied knowledge of ontogeny to the interpretation of phylogeny in trilobites. In contrast, little attempt has been made to apply information about trilobite ontogenies to paleoecology. New information on the ontogeny of a Middle Cambrian ptychoparioid has revealed relationships among the presence of discrete instars, protaspid morphogeny, diversity, and competition in trilobite communities. The presence of discrete instars is correlated with high diversity and low environmental stress, and may be an adaptation to reduce intraspecific competition. Changing intensity of intraspecific competition at the transition from a planktic to benthic mode of life may affect instar discreteness in the ontogeny of a single trilobite species.

A silicified ontogenetic series of an undescribed species of Ehmaniella was recovered by acid dissolution of limestone from the Whirlwind Formation in the Wah Wah Mountains of western Utah. In this paper, the taxon will be referred to as "Ehmaniella sp."

The observed ontogeny of Ehmaniella sp. begins with the protaspid period, which is subdivided into anaprotaspid and metaprotaspid stages. Anaprotaspids fall into two groups that are separated by a distinct morphologic gap. The first group (fig. 1A) is represented by 15 individuals. Length ranges from 0.35 to 0.41 mm, and width ranges from 0.36 to 0.46 mm. In the second group (fig. 1B) containing 29 individuals, length ranges from 0.44 to 0.49 mm and width ranges from 0.45 to 0.51 mm. Members of this group differ from those in the first by having a more oval or subrectangular exoskeleton, more prominent occipital ring, wider posterior notch, and shorter fixigonal spines. Because there are no individuals intermediate in either size or shape (fig. 2), I conclude that these two groups correspond to instars. Also, the groups are normally distributed, as would be expected if they are instars. To my knowledge, this is the first report of distinct instars of the anaprotaspid stage in ptychoparioid trilobites.

The metaprotaspid stage is represented by 78 individuals. Length ranges from 0.49 to 0.63 mm, and width ranges from 0.50 to 0.61 mm. The tests include

two morphotypes, which differ in size as well as shape of the posterior margin of the protopygidium (fig. 1C, D). Specimens intermediate between these two morphotypes are common, and the sample cannot be divided into distinct instars.

Representative early and late meraspid crania show major allometric changes (fig. 1E, F). Holaspid crania of this species (fig. 1G) are similar to those of most previously described species of Ehmaniella (for example Resser, in McKee and Resser, 1945).

Eleven distinct peaks in the size-frequency distribution of meraspid crania of Ehmaniella sp. may represent the modes of successive, partially overlapping instars (fig. 3). Similar peaks were similarly interpreted by Palmer (1957) for the olenellid Paedeumias clarki. An average linear growth ratio between instars of 1.13 was obtained for Ehmaniella sp. compared to 1.15 for P. clarki (Palmer, 1957).

Closely related sympatric species that compete for resources typically exhibit a linear size ratio of about 1.26 (Chapman, 1977). This approximately corresponds to a doubling in volume. The ratio has been explained as a mechanism for resource partitioning between species. Many modern arthropods closely approach a doubling in volume between instars (Przibram, 1931, as cited by Kesling, 1952, p. 772). The increase of dimensions at a constant percentage between successive instars (Dyar's Law) holds in many, though not all, modern arthropods; as well as in some Paleozoic ostracodes (Kesling, 1952); the olenellid Paedeumias clarki (Palmer, 1957); the agnostoid Trinodus elspethi (Hunt, 1967); the corynexochoid Bathyriscus fimbriatus (Robison, 1967); and the ptychoparioid Ehmaniella sp. Hunt (1967, p. 204) reported an average growth increment between instars of from 1.21 to 1.25 for T. elspethi, which approximates the ratio corresponding to a doubling in volume. The mean growth ratio for many arthropods of 1.26 may be a mechanism for resource partitioning between successive instars (Chapman, 1977).

Greater discreteness of instars should be correlated with reduced competition between members of successive instars. Discrete anaprotaspid instars cannot be recognized in Bathyriscus fimbriatus (Robison, 1967, p. 215-216); however, its anaprotaspids display morphologic variation similar to that in anaprotaspids of Ehmaniella sp. Discrete

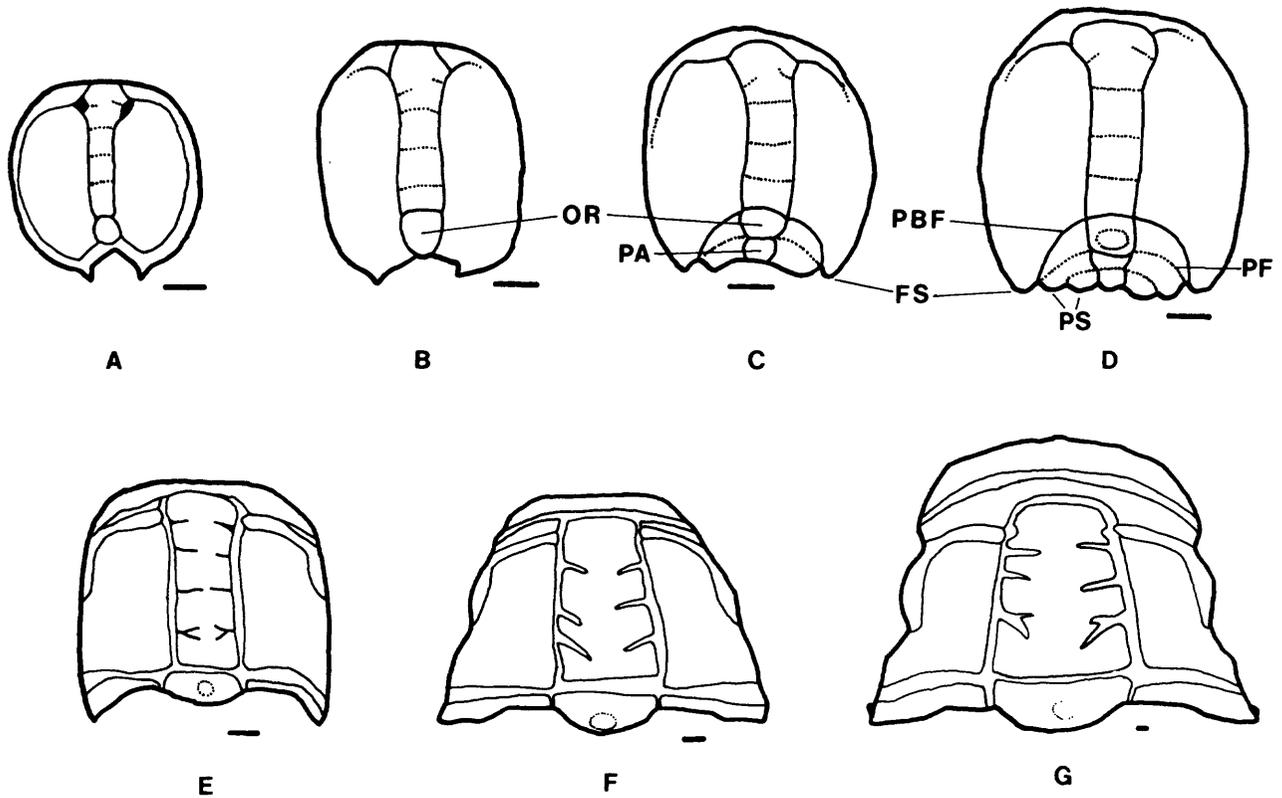


Figure 1.--*Ehmaniella* sp. A, early anaprotaspis; B, late anaprotaspis; C, early metaprotaspis; D, late metaprotaspis; E, early meraspis; F, late meraspis; G, holaspis cranidium; FS, fixigenal spines; OR, occipital ring; PA, axis of protopygidium; PBF, posterior border furrow; PF, protopygidial furrow; PS, protopygidial spines. Scale is 0.1 mm.

metaprotaspis and post-protaspis instars are present in *B. fimbriatus* but not in *Ehmaniella* sp. In *B. fimbriatus* instar discreteness increases with increasing size, whereas in *Ehmaniella* sp. it decreases. Thus, intraspecific competition in *B. fimbriatus* may have been more important and in *Ehmaniella* sp. less important, with increasing size. The mean growth ratio for the first 11 meraspis instars in *Ehmaniella* sp. is 1.13, whereas the mean for the three protaspis instars is 1.21, which represents a greater size difference between instars and suggests a greater need to reduce competition between members of successive protaspis instars. Growth ratios for *B. fimbriatus* are estimated from graphs in Robison (1967). The mean growth ratio for post-anaprotaspis instars of *B. fimbriatus* is 1.17 (the metaprotaspis are included with the cranidia because they also exhibit discrete instars; adjustment is made for the presence of the protopygidium). The corresponding value for *Ehmaniella* sp. is 1.14. The higher ratio for *B. fimbriatus* suggests a greater emphasis on reducing competition between members of successive instars.

Diversity also may be related to competition. Species of modern mollusks in high-diversity

communities tend to exhibit many adaptations interpreted to result from competition or predation, which may be due to the greater number and complexity of biotic interactions in such communities (Vermeij, 1978). Species typical of low-diversity communities, which usually occur in stressful environments, exhibit fewer morphological structures interpreted as adaptations to predation or competition. According to Vermeij, this may result from both the stressed environment, which necessitates complex physiological adaptations to the physico-chemical environment, and the low levels of competition and predation that reduce the need for energetically expensive adaptations to biotic factors.

The physiological control of ecdysis is energetically expensive, and organisms experiencing little selection for precision in timing of ecdysis should not be expected to possess precise hormonal control. Specimens of *B. fimbriatus* are typically found in high-diversity faunas in open-shelf (unrestricted) environments (R. A. Robison, oral comm., 1981) and have discrete post-protaspis instars, although the sample studied by Robison (1967) was taken from a thin bed containing only *B. fimbriatus*. The Whirlwind

Formation, from which the sample of *Ehmaniella* sp. used in this study was collected, represents a restricted lagoonal environment (D. C. Kopaska-Merkel, unpub. data). The Whirlwind contains a low-diversity fauna in which more than 99 percent of all preserved trilobites are *Ehmaniella* sp., which lacks discrete post-protaspid instars. Presumably, precise control of ecdysis is necessary to keep the post-protaspid instars of *B. fimbriatus* discrete, at an unknown but probably significant metabolic cost. The hypothesized correlation between (1) discrete instars, (2) high diversity of benthic trilobites that may have been in competition, and (3) low stress is readily testable by detailed work on other species.

Distinct protaspid instars do not occur in *Crassifimbria walcotti* (Palmer, 1958, p. 169), a ptychoparioid whose anaprotaspid (fig. 4A) is similar to the early anaprotaspid of *Ehmaniella* sp. In contrast, the metaprotaspids of *C. walcotti* and *Ehmaniella* sp. are distinctly different (compare figs. 1C, 1D, and 4B). Metaprotaspids of *C. walcotti* lack fixigenal and protopygidial spines, and their librigenae have migrated to the dorsal surface. The metaprotaspid of *Ehmaniella* sp. bears fixigenal and protopygidial spines, and librigenae remain ventral.

The larvae of *C. walcotti* and *Ehmaniella* sp. are thought to have been planktic, whereas the adults were probably benthic. Protaspids of many trilobite species possess one or more pairs of spines, which disappear during ontogeny. Spines aid flotation in many recent planktic crustacean larvae, and may have had the same function in spinose protaspid trilobites. Most protaspid trilobites have ventral eyes, whereas most holaspids have dorsal eyes. The majority of recent planktic arthropods swim right side up (the fairy shrimp are an exception). In the absence of evidence to the

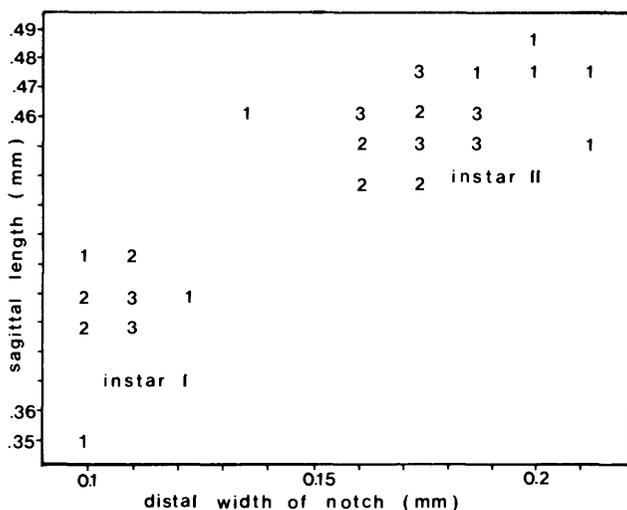


Figure 2.--*Ehmaniella* sp. Sagittal length versus width between posterior spine bases of anaprotaspids. Numerals indicate numbers of individuals at each point.

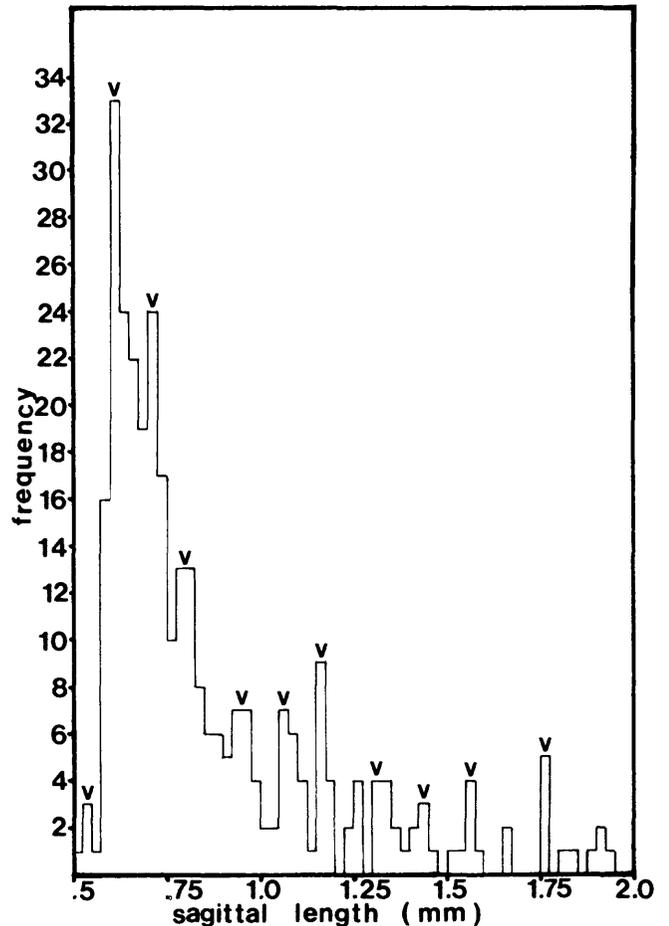


Figure 3.--*Ehmaniella* sp. Size-frequency histogram of 287 meraspid cranidia. "V's" indicate inferred instar modes.

contrary, the *Ehmaniella* protaspids are also assumed to have swum right side up. Metaprotaspids had lateral eyes, and it is unlikely that they swam upside down, because the eyes in the subsequent (benthic) instars quickly assumed a dorsal position. The presence of ventral eyes in the anaprotaspids suggests that they lived high in the water column, and that they detected nearby food particles visually. The metaprotaspid of *C. walcotti* may have lost its spines and acquired dorsal eyes because it had already begun a benthic existence, in contrast to the metaprotaspid of *Ehmaniella* sp. A high level of intraspecific competition in the planktic protaspid stage may have caused selection for discrete instars in *Ehmaniella* sp., possibly as a result of the longer time that specimens spent as planktic larvae.

The presence of discrete protaspid instars and the lack of discrete postprotaspid instars in *Ehmaniella* sp. may be explained in terms of intraspecific resource partitioning.

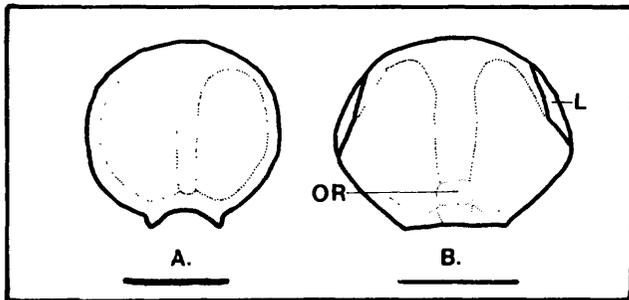


Figure 4.--Crassifimbria walcotti. A, anaprotaspid; B, metaprotaspid. L, librigena; OR, occipital ring. Modified from Palmer (1958). Scale is 0.25 mm.

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## 34. THE CAMBRIAN-ORDOVICIAN BOUNDARY IN MISSOURI AS DETERMINED BY CONODONTS

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The position of the Cambrian-Ordovician boundary in Missouri has been placed at the contact between the Eminence and Gasconade Dolomites and above an "upper Eminence fauna," following the work of Dake (1930) and Bridge (1930). However, the faunal "zones" of Bridge (1930) are based largely on conodont specimens collected from float. Howe and others (1972) first questioned Bridge's placement of the boundary because *Plethopeltis*, a genus previously considered only of Cambrian age and common in the upper Eminence, was reported from Lower Ordovician rocks in Wisconsin by Davis (1970) and in Oklahoma by Stitt (1971). Later, Stitt (1977, p. 28, 29) discussed the faunas reported from the upper Eminence of Missouri and the problems of building a biostratigraphic zonation from fossils found mostly in float. He noted that *Plethopeltis* and *Entomaspis* are found above the fauna reported by Bridge (1930, p. 95) as occurring from 25 to 30 m below the top of the Eminence. This latter fauna is definitely Cambrian in age and is similar to the *Saukiella serotina* or *Saukiella junia* Subzone of the *Saukia* Zone from Texas and Oklahoma (Stitt, 1977). Stitt also mentioned that in float samples he has collected in Missouri, *Plethopeltis* does not occur with any known Cambrian trilobites in the same chert sample.

Conodonts have been obtained from the Eminence and Gasconade Dolomites only in the Lake of the Ozarks region near Camdenton in central Missouri (fig. 1). Recoveries are on the order of five specimens per kilogram. Samples from elsewhere in the state have been barren. The host rocks are highly recrystallized dolomites having little evidence of internal structure. Most rocks do show faint laminae, that are interpreted as planar stromatolite structure and suggest intertidal to supratidal depositional environments. The few beds from which conodonts have been recovered do not appear to be laminated. The overall picture is one of a broad carbonate shelf in which environments were dominantly hypersaline and otherwise inhospitable.

Dolomites, such as dealt with in this study, react slowly with acetic acid, and several weeks are needed to get a reasonable breakdown of the rock. Conodonts can then be separated from the residue of dolomite rhombs even though the specific gravities are nearly the same. By using a single dolomite crystal or

cleavage fragment as a standard, the specific gravity of tetrabromoethane can be adjusted with white kerosene so that only 1 to 5 percent of the dolomite settles with the conodonts.



Figure 1.-- Eminence and Gasconade conodont localities in Missouri.

### LITHOLOGIC SUCCESSION

In the Lake of the Ozarks region, the Eminence is mostly stromatolitic dolomite. The basal part of the Gasconade is quartz sandstone (Gunter Sandstone Member). The overlying Gasconade dolomites are similar to the Eminence but may have more chert. The Eminence-Gasconade contact is sharp, may show a microrelief of a few centimeters, and is considered to be a disconformity. Ball and Smith (1903) reported pebbles of Eminence in the basal Gunter from the Lake of the Ozarks region, and Bridge (1930) found waterworn chert pebbles at the base of the Gunter from Shannon County in southeastern Missouri.

FAUNAL SUCCESSION

Conodont faunas A, B, and C were proposed by Ethington and Clark (1971). Fauna A is the same as the Cordylodus proavus Zone of Miller (1980). Miller (1980) divided the Cordylodus proavus Zone into five subzones, which are, in ascending order, Hirsutodontus hirsutus, Fryxellodontus inornatus, Clavohamulus elongatus, Hirsutodontus simplex, and Clavohamulus hintzei subzones. He also correlated the conodont subzones with trilobite zones of Winston and Nicholls (1967) and Longacre (1970) for the Llano uplift in Texas, and Stitt (1977) for the Wichita Mountains in Oklahoma (fig. 2).

Figure 3 shows the stratigraphic distribution of conodont faunas discussed in this report. The lowest collection contains only Teridontus nakamurai, a species that first appeared in North American shallow-shelf sequences at the base of the Cordylodus proavus Zone. The next higher collection, 7 m below the top of the Eminence, has Teridontus nakamurai, Cordylodus proavus, and Fryxellodontus lineatus (planar element). The latter element occurs only in the Fryxellodontus inornatus and Clavohamulus elongatus subzones of the Cordylodus proavus Zone. Collections from 3 m below the top of the Eminence and from the uppermost 20 cm of the formation yield only Teridontus nakamurai.

The Gunter Sandstone Member of the Gasconade Dolomite did not yield conodonts, and the lowest collection from the Gasconade occurs just above the Gunter in the basal 30 cm of Gasconade Dolomite, or about 8 m above the base of the Gasconade Dolomite. This collection yielded Cordylodus drucei, Acontiodus iowensis, Utahconus sp., "Scolopodus" n. sp. 1, and Teridontus nakamurai, a lower fauna B (Miller, 1980).

Fauna C is represented by conodonts from 23 m above the base of the Gasconade Dolomite in a dolomitized calcarenite. Loxodus bransoni, a species diagnostic of fauna C (Ethington and Clark, 1971), occurs with Paltodus bassleri, P. variabilis, Drepanodus sp., "Scolopodus" n. sp. 2, and genus and species undet.

CAMBRIAN-ORDOVICIAN BOUNDARY

Late Cambrian depositional rates in the Lake of the Ozarks region were erratic (Thacker, 1974). Thickness of the interval from the Eoorthis coquina to the top of the Cambrian rocks ranges from 175 to 200 m as compared to 146 m for the same interval in the Threadgill Creek section in Texas (J. F. Miller, personal communication). Thus, the Missouri section indicates depositional rates from 20 to 25 percent greater than the Texas section.

Assuming that the depositional rates were constant for each area for a short time into the Lower

System	Series	Trilobite Zone		Conodont Zone	
		Trilobite Subzone	Conodont Subzone		
ORDOVICIAN	Canadian	<i>Symphysurina</i>	<i>Symphysurina bulbosa</i>	Conodont Fauna B	
			<i>Symphysurina brevispicata</i>		
		<i>Missisquoia</i>	<i>Missisquoia typicalis</i>		<i>Clavohamulus elongatus</i>
			<i>M. depressa</i>		<i>Fryxellodontus inornatus</i>
	Croixian	<i>Saukia</i>	<i>Corbinia apopsis</i>	<i>Hirsutodontus hirsutus</i>	<i>Cordylodus proavus</i>
			<i>Saukiella serotina</i>	<i>Cambroistodus minutus</i>	
			<i>Saukiella junia</i>	<i>Eoconodontus notchpeakensis</i>	
			<i>Saukiella pyrene</i>	<i>Proconodontus muelleri</i>	
CROIXIAN	Croixian	<i>Ellipsocephaloides</i> Zone	<i>Proconodontus posterocostatus</i>	<i>Proconodontus</i>	
			No zonation established		

Figure 2.--Conodont and trilobite zonation for the upper Croixian and lower Canadian Series (after Miller, 1980).

Ordovician, it is possible to approximate the lowest and highest probable positions of the Cambrian-Ordovician boundary in Missouri. The following calculations for the Missouri section are rounded to the nearest meter. In Texas, Fryxellodontus lineatus (planar element) ranges from 1 to 7 m above the

Cambrian-Ordovician boundary and is restricted to the Fryxellodontus inornatus and Clavohamulus elongatus subzones of the Cordylodus proavus Zone (J. F. Miller, personal communication). Therefore, the highest probable position of the Cambrian-Ordovician boundary in Missouri is 1 m below the occurrence of F. lineatus (planar element), or 8 m below the top of the Eminence. The lowest probable position is 10 m below F. lineatus (planar element), or 17 m below the top of the Eminence. The base of the Cordylodus proavus Zone would then range from 11 m to 18 m below the top of the Eminence. The amount of unrecorded geologic time at the unconformity between the Eminence and Gasconade is probably small. Most likely only the upper part of the Cordylodus proavus Zone is missing.

Part of the expenses for the field work were defrayed by a grant from the Faculty Development Fund, Southwest Missouri State University. I express special thanks to J. F. Miller for his assistance in this project.

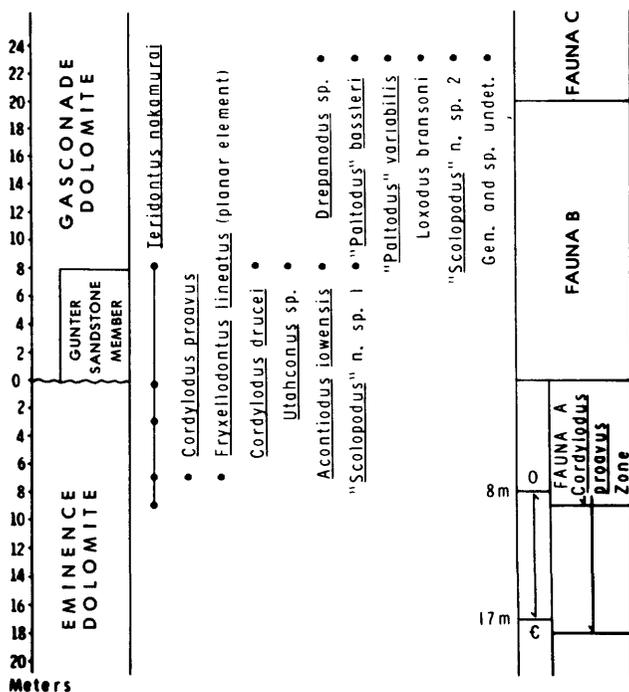


Figure 3.--Ranges of conodont taxa from the upper Eminence and lower Gasconade Formations.

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# 35. ZONATION OF CAMBRIAN FAUNAS IN WESTERN ZHEJIANG<sup>1</sup> AND THEIR CORRELATION WITH FAUNAS IN NORTH CHINA, AUSTRALIA, AND SWEDEN

By

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Western Zhejiang is the Cambrian stratotype locality of the Southeast China Faunal Province, where the following five stratigraphic units and fossil zones with key genera and species are recognized:

## UPPER CAMBRIAN

### V. Siyangshan Formation

15. Lotagnostus hedini Zone: Lotagnostus hedini, Plicatolina changshanensis, P. inflexa (sp. nov.)
14. Lotagnostus punctatus Zone, including:
  - b. Acaroceras endogastrum Subzone: Acaroceras elongatum, A. endogastrum, Ectenclites primus, E. penecilin, Zhuibianoceras conicum, Huaiheceras hanjiaensis, Lotagnostus punctatus.
  - a. Hedinaspis Subzone: Lotagnostus punctatus, L. asiaticus, Rhaptagnostus changshanensis, Pseudagnostus rugosus, Geragnostus (Micragnostus) orientalis, Hedinaspis regalis, Wujiajiania expansa, Charchaia norini, Pseudoyuepingia zhejiangensis, Proceratopyge (Sinoproceratopyge) constrictus, Promacropyge carinata, Jegorovaia expansa, Olenus sinensis, Chekiangaspis chekiangensis, Onchonotina vigilans.

### IV. Huayansi Formation

13. Pseudoglyptagnostus clavatus-Sinoproceratopyge kiangshanensis Zone: Pseudoglyptagnostus clavatus, Peratagnostus zhejiangensis (sp. nov.), Xestagnostus transversus (sp. nov.), Proceratopyge (Sinoproceratopyge) kiangshanensis, P. (S.) sinuatus (sp. nov.), P. (S.) distincta (sp. nov.), P. (P.) mirabilis (sp. nov.), P. (P.) distensus (sp. nov.).
12. Erixanium Zone: Erixanium rectangularis (sp. nov.), Pseudagnostus idalis, P. vigilans (sp. nov.).

11. Proceratopyge fenghwanqensis Zone: Proceratopyge (Proceratopyge) fenghwanqensis, P. (Sinoproceratopyge) changshanensis (sp. nov.), Pseudagnostus idalis, P. vigilans (sp. nov.), P. cf. cyclopyge, Peratagnostus distinctus (sp. nov.).
10. Glyptagnostus reticulatus Zone: Glyptagnostus reticulatus reticulatus, G. r. angelini, Pseudagnostus vigilans (sp. nov.), P. cf. mestus, Kormagnostus(?) clavatus (sp. nov.), Aspidagnostus chekiangensis, A. cf. stictus.
9. Glyptagnostus stolidotus Zone: Glyptagnostus stolidotus, G. sp., Aspidagnostus chekiangensis, A. pentagonalis (sp. nov.), Clavagnostus subconicus (sp. nov.), C. (Clavagnostotes) sp., Tomagnostella tianmashanensis (sp. nov.), Pseudagnostus cf. bulgosus, Proceratopyge zhejiangensis (sp. nov.), P. conifrons, Kormagnostus(?) clavatus (sp. nov.), Homagnostus sp., Paradamesella sp., Teinistion sp.
8. Lejopyge sinensis Zone: Lejopyge sinensis (sp. nov.), Goniagnostus (Allobodochus) nodibundus, Ciceragnostus(?) sp., Oidalagnostus tienshanensis, Cyclagnostus yaogongbuensis (sp. nov.), Ammagnostus duibianensis (sp. nov.), Proceratopyge fuyangensis (sp. nov.), Fuyangia fengzuensis (gen. and sp. nov.), F. miranda (gen and sp. nov.), Buttsia globosa (sp. nov.), Bergeronites hunanensis.

## MIDDLE CAMBRIAN

### III. Yangliugang Group

7. Lejopyge armata Zone:  
Upper part: Lejopyge armata, Goniagnostus (Allobodochus) spiniger, Ovalagnostus changi, Fuchouia oratolimbata, Proceratopyge conifrons.  
Middle part: Lejopyge armata, Goniagnostus

<sup>1</sup>Previously Chekiang Province.

	NORTH CHINA PROVINCE		WESTERN ZHEJIANG		AUSTRALIA *		SWEDEN **					
	Stages and Zones		Stages and Zones		Stages and Zones		Stages and Zones					
Upper Cambrian	Fengshan Stage	<i>Mictosaukia orientalis</i>	Siyangshan Formation	<i>Lotagnostus punctatus</i>	Payntonian		<i>Acerocare</i>					
		<i>Sinoeremoceras</i>							<i>Lotagnostus hedini</i>	pre-Payntonian A	<i>Peltura scarabaeoides</i>	
		<i>Quadratrice phalus</i>							<i>Acaroceras endogastrum</i> Subzone			
		<i>Ptychaspis-Tsinania</i>							<i>Hedinaspis</i> Subzone			
	Changshan Stage	<i>Kaolishania</i>	Huayansi Formation	Idamean	pre-Payntonian B post-Idamean	<i>Peltura minor</i>						
		<i>Changshania</i>							<i>Pseudoglyptagnostus clavatus</i> – <i>Sinoproceratopyge kangshanensis</i>	<i>Irvingella tropica</i> <i>Agnostotes inconstans</i>	<i>Protopeltura praecursor</i>	
		<i>Chuangia</i>							<i>Erixanium</i>	<i>Stigmatoa diloma</i>		<i>Leptoplastus</i>
	Kushan Stage	<i>Drepanura</i>	<i>Proceratopyge fenghwangensis</i>	<i>Erixanium sentum</i>	<i>Parabolina spinulosa</i>	<i>Homagnostus obesus</i>						
		<i>Blackwelderia</i>	<i>Glyptagnostus reticulatus</i>	<i>Proceratopyge cryptica</i>	<i>Glyptagnostus reticulatus</i>							
			<i>Glyptagnostus stolidotus</i>	<i>Glyptagnostus stolidotus</i>	<i>Glyptagnostus stolidotus</i>				<i>Agnostus pisi forms</i>			
	<i>Lejopyge sinensis</i>	Mindyailan	<i>Cyclagnostus quasivespa</i>	<i>Erediaspis eretes</i>								
Middle Cambrian	Changhia Stage	<i>Damesella-Yabeia</i>	Yangliugang Group	<i>Lejopyge armata</i>	Upper part	Boomerangian	Paradoxides forchhammeri	<i>Lejopyge laevigata</i>				
		<i>Amphoton – Taitzuia</i>							Middle part	<i>Damesella torosa –</i> <i>Ascionepea janitrix</i>	<i>Jincella brachymetopa</i>	
		<i>Crepicephalina</i>							Lower part	<i>Lejopyge laevigata</i> III		
										<i>Lejopyge laevigata</i> II		
	Hsuehuang Stage	<i>Bailiella</i>	Yangliugang Group	Florin	Templetonian	<i>Triplagnostus gibbus</i>		<i>Paradoxides paradoxissimus</i>	<i>Triplagnostus lundgreni –</i> <i>Goniagnostus nathorsti</i>			
		<i>Poriagraulos nanum</i>								<i>Pseudophalacroma triangularis</i>	<i>Goniagnostus nathorsti</i>	
		<i>Sunaspis</i>								<i>Ptychagnostus atavus</i>	<i>Doryagnostus notalibrae</i>	<i>Ptychagnostus punctuosus</i>
		<i>Hsuehuangia – Ruichengella</i>								<i>Triplagnostus gibbus</i>	<i>Ptychagnostus punctuosus</i>	<i>Euagnostus opimus</i>
											<i>Ptychagnostus atavus</i>	<i>Euagnostus opimus</i>
											<i>Triplagnostus gibbus</i>	<i>Euagnostus opimus</i>
			<i>Euagnostus opimus</i>	<i>Hypagnostus parvifrons</i>								
			<i>Peronopsis longinqua</i>	<i>Tomagnostus fissus –</i> <i>Ptychagnostus atavus</i>								
				<i>Triplagnostus gibbus</i>	<i>Triplagnostus gibbus</i>							
					<i>Eccaparadoxides oelandicus</i>	<i>Eccaparadoxides pinus</i>						
					<i>Eccaparadoxides oelandicus</i>	<i>Eccaparadoxides insularis</i>						

\* Mainly after Öpik (1967, 1979), Henderson (1976), and Shergold (1975)  
 \*\* Adopted from Martinsson (1974)

Figure 1.--Correlation chart of Middle and Upper Cambrian in western Zhejiang, north China, Australia, and Sweden.

(Allobodochus) spiniger, Hypagnostus brevifrons, H. cf. correctus, Tomagnostella jiangshanensis (sp. nov.), Phalagnostus carinatus (sp. nov.), Peronopsis sp. 1, Clavagnostus (Clavagnostotes) lanceolatus (subgen. and sp. nov.), C. (Clavagnostotes) rarus (subgen. and sp. nov.), Diplagnostus zhexiensis (sp. nov.), D. planicauda vestgothicus, Ovalagnostus personatus, Fuchouia oratolimbata, Pianaspis sinensis, Paradamesella nobilis (sp. nov.), Baojingia daichenensis (sp. nov.).

Lower part: Lejopyge armata, L. laevigata, Ptychagnostus aculeatus, Linguagnostus transversus (sp. nov.), L. spinosus.

Ovalagnostus bispiniformis, Goniagnostus (Allobodochus) spiniger, Tomagnostella jiangshanensis (sp. nov.), Fuchouia oratolimbata, F. chiai, Hypagnostus hunanicus, Pseudophalacroma dubium, Diplagnostus zhexiensis (sp. nov.).

6. Pseudophalacroma triangularis Zone: Pseudophalacroma triangularis, P. dubium, Goniagnostus (Allobodochus) spiniger, Hypagnostus hunanicus, Tomagnostella jiangshanensis (sp. nov.), Diplagnostus floralis, Fuchouia oratolimbata.

5. Ptychagnostus atavus Zone: Ptychagnostus atavus, P. cf. sinicus.

4. Triplagnostus gibbus Zone: Triplagnostus gibbus, T. sp.

## LOWER CAMBRIAN

### II. Dachenling Formation

3. Arthricocephalites-Changaspis Zone: Arthricocephalus (Arthricocephalites) granulus, A. (A.) sp., Changaspis placenta.

### I. Hotang Formation

2. Shabaella Zone: Shabaella jiangshanensis, S. cenvexa, S. fengzuensis (sp. nov.), Sinolenus hotangensis, S. brevis, Hunanocephalus (Doutingia) (?) rarus, H. (D.X?) constrictus.
1. Hunanocephalus Zone: Hunanocephalus ovalis.

The faunas of the Lower Cambrian contain many endemic forms, most of which are also dominant in the eastern margin of the Yangtze Subprovince and in the Transitional Province.

Correlation of the Middle and Upper Cambrian in Western Zhejiang, North China, Australia, and Sweden is tabulated in figure 1.

## 36. SUMMARY OF THE CAMBRIAN BIOSTRATIGRAPHY OF CHINA

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Recent revision of the Cambrian biostratigraphy of China resulted in the recognition of 10 stages and 31 faunal zones. They include:

### Upper Cambrian Series

- X. Fengshan Stage: 31, Mictosaukia orientalis Zone; 30, Sinoeremoceras Zone; 29, Quadraticephalus Zone; 28, Ptychaspis-Tsinania Zone.
- IX. Changshan Stage: 27, Kaolishania Zone; 26, Changshania Zone; 25, Chuangia Zone.
- VIII. Kushan Stage: 24, Drepanura Zone; 23, Blackwelderia Zone.

### Middle Cambrian Series

- VII. Changhia Stage: 22, Damesella-Yabeia Zone; 21, Amphoton-Taitzuia Zone; 20, Crepicephalina Zone; 19, Lioparia<sup>1</sup> Zone.
- VI. Hsichuang Stage: 18, Bailiella Zone; 17, Poriagraulos nanum Zone; 16, Sunaspis Zone; 15, Hsichuangia-Ruichangella Zone<sup>2</sup>.

### Lower Cambrian Series

- V. Maochuang Stage: 14, Shantungaspis Zone; 13, Yaojiayueella Zone.
- IV. Lungwangmiao Stage: 12, Redlichia nobilis Zone; 11, Redlichia murakamii-Hoffetella Zone.
- III. Tsanglangpu Stage: 10, Megapalaeolenus Zone; 9, Palaeolenus Zone; 8, Paokannia-Sichuanolenus Zone; 7, Drepanuroides Zone; 6, Yunnanaspis-Yiliangella Zone.

<sup>1</sup>Liaoyangaspis Chang, 1959, and Pseudoliostroacina Kobayashi, 1938, are synonymous with Lioparia Lorenz, 1906; therefore, the Liaoyangaspis Zone established by Chang in 1959 is automatically replaced by the Lioparia Zone.

<sup>2</sup>Hsichuangia-Ruichangella Zone is here used to substitute the Kochaspis hsichuangensis Zone established by Lu in 1954. The last named species is the type species of the genus Hsichuangia Lu, 1981.

- II. Chiungchussu Stage: 5, Yunnanocephalus-Malungia Zone; 4, Epredlichia-Wutingaspis Zone; 3, Parabadiella-Mianxiandiscus Zone.
- I. Meishucun Stage: 2, Siphogonuchites-Zhijinites-Sachites Assemblage; 1, Anabarites-Circotheca-Protohertzina Assemblage.

The above stages and faunal zones or assemblages are chiefly based on the Cambrian strata in north and northeast China and in the Yangzi region. They cannot be used in southeast and northwest China because the biofacies and lithofacies are different there. The zonation and correlation of the latter regions are given in a separate report by Lu and Lin (this volume).

### BOUNDARIES OF THE CAMBRIAN SYSTEM IN CHINA

The most complete Lower Cambrian sequences directly overlying the Sinian strata are the Meishucun Formation in Eastern Yunnan, the Meideiping Formation in Western Sichuan, and the Huangshandong Formation in the gorge district of the Yangzi. The Precambrian-Cambrian boundary is at the base of the Anabarites-Circotheca-Protohertzina Assemblage in Eastern Yunnan, or at the base of the Protoconus crestatus-Eosoconus primarius Assemblage in the Yangzi gorge<sup>3</sup>. In the Jiangnan region, the Lower Cambrian begins with anthracitic coal, overlain by black shale and siliceous beds containing abundant sponge spicules and a few trilobites, such as Hunanocephalus, Shabaella, and Sinolenus, and then succeeded by dark-gray carbonates containing Arthricocephalus and Changaspis. In south China, the

<sup>3</sup>According to Yu Wen (1979), the Huangshandong Formation in the Yangzi gorge has three assemblages: The lower, Protoconus crestatus-Eosoconus primarius; the middle, Yangtzeconus priscus-Archaeospira ornata; and the upper, Truncatoconus yichangensis-Cambrospira-sinensis.

Sinian and Cambrian are chiefly composed of turbidites that contain a very few sponge spicules in the Lower Cambrian; therefore the section is not adequate for the resolution of the boundary problem. In north and northeast China, there is a major hiatus between the Precambrian and Cambrian. The Meishucun, the Chiungchussu, and the lower part of the Tsanglangpu Stages are entirely absent. The middle Lower Cambrian strata with fossils of the Bergeroniellus, Palaeolenus, and Megapalaeolenus Zones overlap unconformably on the older Proterozoic and Archaean rocks.

No agreement has been reached on the boundary between the Lower and Middle Cambrian in northern China. When they erected the name "Maochuang Stage" in 1954, Lu and Tong put it at the top of the Lower Cambrian, whereas Xiang and others (1979) and Zhang (1980) regarded it as the base of the Middle Cambrian. Recently, Redlichia has been found in the lower part of the Maochuang Stage. This genus has for a long time been considered as a precise guide fossil to the Early Cambrian of the oriental fauna. The problem of the age of the upper part still remains to be settled.

No disagreement exists on the separation of the Middle and Upper Cambrian in China since 1937 when Sun placed the boundary between the Changhia and Kushan Stages.

The Cambrian-Ordovician boundary in China is definitely known in two different localities. The boundary is placed between the Lotagnostus hedini Zone and the Hysterolenus Zone in western Zhejiang and Ningxia, and the boundary is between the Mictosaukia orientalis Assemblage and the Onychopyge-Alloleiostrigium Assemblage in Hebei and Liaoning.

#### FAUNAL PROVINCIALITY

Through the study by Lu and others in 1974, the Cambrian faunas of the world can be separated into two major faunal realms: the Oriental Fauna and the Occidental Fauna. The former is subdivided into the North China Province, the Southeast China Province

and the Transitional Province. According to the different sedimentological characteristics, the North China Province may be divided into two subprovinces: the North China-Southern Northeast China Subprovince and the Yangzi-Qinghai-Xizhang (Tibet) Subprovince. The Southeast China Province includes the Jiangnan-Northwestern China Subprovince and the Zhujiang Subprovince.

The environment in the North China-Southern Northeast China Subprovince was mainly benthic in shallow seas; the environments were variable, having had warm to rather hot climatic and oxidizing conditions. The organisms, trilobites in particular, were very abundant and show a rapid rate of evolution and extinction in a normal marine habitat. In the Yangzi-Qinghai-Xizhang Subprovince, the earliest Cambrian seas contained more phosphorus, and the small shelly animals were very luxuriant, and were dominated by benthic and neritic forms. The Middle and Upper Cambrian seas were restricted, as indicated by the presence of a very thick dolomite sequence and by the rarity of animal remains. In the Jiangnan-Northwestern China Subprovince, the Early Cambrian was dominated by strong reducing environments, and phosphorus nodules, anthracites, siliceous rocks, and black carbonates were deposited; fossils are rarely present. In the Middle and Upper Cambrian, the environments were still reducing, and are chiefly characterized by black or grayish-black carbonates. Abundant floating trilobites lived then, such as agnostids and olenids, most of which were quite different compared to those of the North China Province. Obviously, these trilobites were adapted to a habitat of deep troughs and basins. In the Zhujiang Subprovince, the sea was highly turbid and extremely shallow; the strata are very thick flysch or paraflysch. This type of environment was apparently unfavorable to life; only a few floating organisms from the Jiangnan area existed.

Between all the provinces and subprovinces, there were transitional areas where biofacies and lithofacies were intermingled.

The geological and geographical distributions of anthracite and phosphorus, vanadium, molybdenum, copper, nickel, cobalt and uranium ores in China are obviously related to these provinces, as discussed by Lu in 1979.

## 37. A SYNOPSIS OF THE CAMBRIAN SYSTEM IN YUNNAN, CHINA

By

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Rocks of the Cambrian System are relatively well developed and widespread in Yunnan. The Early Cambrian is completely developed and is represented by a variety of sedimentary rocks whose faunas have served as the standard for the Lower Cambrian zonation of China. Based on sedimentological characters, thicknesses, faunal differences, and inferred paleogeography, the Cambrian System in Yunnan is divided into two major sedimentary provinces; the Yangtze Province and the Western Yunnan Province. The Yangtze Province can be further subdivided into four subprovinces: eastern Yunnan, north-central Yunnan, northeastern Yunnan, and southeastern Yunnan. Eastern and southeastern Yunnan have been well studied and they may be further divided into some smaller areas. The Western Yunnan Province is divisible into two areas, the Baoshan and Mangshi areas.

The Early Cambrian is best developed in the eastern Yunnan subprovince, while Middle and Late Cambrian are best developed in the southeastern Yunnan subprovince. The Cambrian System is divided into 10 formations and 25 fossil zones (table 1).

In the eastern Yunnan subprovince, the Early and Middle Cambrian beds form a continuous sequence with the underlying Sinian System. The Meishucun Stage, at the base of the Cambrian, contains abundant shelly fossils and trace fossils. In the Xiaowaitaushan Member of the Meishucun Formation, the basal beds, containing the *Anabarites primitivus* Subassemblage, rest on the Denging Formation and mark the boundary between the Sinian and Cambrian in China.

In southeastern Yunnan, the Cambrian System, which is fully developed and thicker than elsewhere, seems faunally and sedimentologically to belong to the Yangtze Province. Although this marginal region between China and Vietnam has been studied and divided into fossil zones by Deprat (1915), Mansuy (1915, 1916), Jacob and Bourrent (1920), Kobayashi (1944, 1967) and Saurin (1956), there are many contradictions. The work of the past 20 years has resulted in the nomenclature and biostratigraphy mentioned above.

In the western Yunnan province, the Lower and Middle Cambrian strata are clastics, and only rare protospongia spicules have been found. However, the

Upper Cambrian includes three abundantly fossiliferous formations and has provided a basis for biostratigraphic zonation.

The Cambrian System of Yunnan includes a variety of siliceous clastics and carbonates. Associated with them throughout the Cambrian are deposits of phosphate, oil shale, gypsum, rare-earth metals, and other metals. Their distribution is affected by the paleogeography and paleoecology, which were controlled by crustal movements and by paleoclimatic changes. Paleogeographic changes permit the Cambrian System to be divided into three sharply separated parts.

The Cambrian biota, which is dominated by trilobites, is mainly of the north China type. However, there are mixed-facies faunas in the Baoshan region, including a few members of the southeast China type; and in the Mangshi region, the faunas are mainly of the southeast China type with a few north China members.

Lower and Middle Cambrian rocks can be correlated to those in other provinces such as Sichuan, Guizhou, and Hubei, and are extremely similar to those of nearby countries such as Vietnam, Burma, and Pakistan. Therefore, study of the Cambrian System of Yunnan will provide an important base for correlation both within China and with other countries.

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Cambrian System	Upper Cambrian	Fengshan stage	Bocaitian form.	Calvinella zone Guangnania zone Prosaukia zone
		Changshan stage	Tangjiaba form.	Kaolishania zone Irvingella zone Chuangia zone
		Kushan stage	Xiechang form.	Blackwelderia-Paralorenzella zone
	Middle Cambrian	Changhsia stage	Longha form.	Damesella zone Taitzuia zone Solenoparops zone
		Hsuchuang stage	Tianpeng form.	Bailiella zone Kaotaia zone
		Maochuang stage	Dayakou form.	Plesiagraulos zone Mengzia zone
	Lower Cambrian	Lungwangmiao stage	Lungwangmiao form.	R. (Pteroredlichia) murakamii zone Hoffetella zone
		Tsanglangpu stage	Tsanglangpu form.	Megapalaeolenus zone Palaeolenus zone Drepanuroides zone Yunnanaspis-Yiliangella zone
		Chiungchussu stage	Chiungchussu form.	Eoredlichia zone Parabadiella zone
		Meishucun stage	Meishucun form.	Eonovitatus-Sinosachites zone Paragloborilus-Siphogonuchites zone Circotheca-Conotheca-Anabarites zone

Table 1.--Chart showing the subdivisions of strata and fossil zones in Yunnan.

		Yangtze province				W. YUNNAN
		E. Yunnan	N.C. Yunnan	NE. Yunnan	SE. Yunnan	
Cambrian System	Upper Cambrian	Erdaoshui form.		Loushanguan group	Bocaitian form.	Baoshan form.
					Tangjiaba form.	Liushui form.
					Xiechang form.	Hetaoping form.
					Longha form.	Gongyanghe group
	Tianpeng form.					
	Dayakou form.					
	Dayakou form.					
	Dayakou form.					
	Dayakou form.					
	Lower Cambrian	Lungwangmiao form.		Qingxudong form.	Dazhai form.	
Tsanglangpu form.		Tsanglangpu form.	Chintingshan form. Minghsinssu form.	Chongzhuang form.		
Chiungchussu form.		Chiungchussu form.	Niuti <del>s</del> ang form.	Maomaotou form.		
Meishucun form.		Meishucun form.	Yankong form.	Langmu <del>o</del> iao form.		

Table 2.--Chart showing correlation of Cambrian strata in the sedimentary provinces and subprovinces of Yunnan.

## 38. THE ROLE OF PAEDOMORPHOSIS IN THE EVOLUTION OF CAMBRIAN TRILOBITES

By

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Discussion of the role that paedomorphosis has played in the evolution of Cambrian and later trilobites has, in the past, centered around the suggested paedomorphic development of particular major morphological features, such as proparian sutures (Stubblefield, 1960) and schizochroal eyes (Clarkson, 1975). However, in recent years attention has migrated to consideration of the evolution of the whole organism and the importance of paedomorphosis in the establishment of new morphotypes.

Paedomorphosis, that is, retention of ancestral juvenile characters in the descendant adult, results from a number of different processes which affect the onset or timing of morphological development. Regulatory gene changes affecting allometric growth rates or altering the timing of onset of maturity, can result in the development of morphotypes quite distinct from the ancestral form, but whose structural genes are almost identical.

As for other groups of organisms, the Cambrian was a time of relatively rapid development of large numbers of trilobite morphotypes. I believe that paedomorphosis may have contributed to this rapid development, particularly during the early part of the Cambrian, by utilizing morphological characters implicit at different ontogenetic stages. Trilobites were thus able, with great economy, to develop appreciably new adult shapes, which were really just modified juvenile character states shunted into the adult states.

There are three ways that such paedomorphosis can occur. The first, and perhaps the simplest, was progenesis--the ability to become sexually mature at an early stage of somatic development. Onset of sexual maturity is characterised by a severe reduction or cessation of growth, both in morphology and size. Thus, if the juvenile phase was shortened by earlier onset of maturity, less time was spent in rapid (juvenile) size increase, and the resultant adult was smaller, and morphologically less developed.

The second way in which juvenile characters can be retained is by neoteny. If the rate of morphological development of the whole animal, or maybe only certain parts of it, is reduced, at the onset of maturity it will not have developed as much as an ancestor that had a faster rate of morphological development.

Often the onset of sexual maturity is delayed, in addition to this reduced rate of morphological development. The descendant adult then is larger than the ancestral adult, because of a longer phase of rapid juvenile size increase.

Progenesis and neoteny can, ideally, produce descendant adults that retain all ancestral juvenile features. Such complete retention is generally the result of progenesis, but only certain morphological characters may be affected by reduced morphological development. Depending on the organ which is retarded and the number of organs affected, various permutations and combinations could produce a vast range of morphotypes.

Although progenetic and neotenic forms may have similar morphology, they may vary appreciably in size. Progenetic forms may be smaller than ancestral adults, and neotenic forms may be as large or larger than ancestral adults, depending on whether or not onset of sexual maturity was also a retarded character.

A third process resulting in paedomorphosis involves a change in the timing of onset of growth of one or a number of characters; this has been termed displacement (Alberch and others, 1979). If the onset of growth is delayed, and the rate of morphological development is consistent with that of the ancestral form, the character will be relatively retarded at maturity. Combined with a reduced rate of development (neoteny), substantial retardation in development may occur, resulting in a mature morphology quite different from the ancestral form, due to an early deviation from the ancestral allometric growth pattern.

The relative importance of these paedomorphic processes in the evolution of trilobites during the Cambrian are discussed below. This discussion, I believe, may bear upon the problems of supra-specific classification in olenellid and other Early Cambrian trilobites, recently outlined by Palmer and Halley (1979).

In interpreting the evolution of five species of *Olenellus* which occur in northwestern Scotland, I used a paedomorphic evolutionary model (McNamara, 1978). From an ancestral morphotype (*O. lapworthi*,

which may be said to pass morphological stages A to K during its ontogeny), four species evolved by progenesis at different stages of the ancestral ontogenetic pathway. O. armatus may be thought of as only having progressed morphologically A-C, O. intermedius A-E, O. hamoculus A-G, and O. reticulatus A-I.

During their ontogeny, trilobites had large numbers of instars (for example Palmer, 1957, suggested that O. gilberti underwent ecdysis at least 29 times during its ontogeny). Each ecdysis during the meraspid period represents a morphological progression and, hence, a potential departure point for progenesis. However, only a restricted number of points of progenesis produce viable species; one interpretation for this is the controlled effect of ecological separation. Sufficient morphological and size separation is required to avoid inhibitive competition between morphotypes.

Benthic trilobites, such as those having O. lapworthi morphology, are likely to have the pelagic juvenile phases. Thus, the morphological distance between the juvenile and adult morphotypes may be great. Juvenile characters retained by some progenetic olenellids, such as O. armatus, include short, anteriorly positioned eyes, spinose cephalon with narrow genal region, small frontal lobe, broad axis, and narrow thoracic pleurae, suggesting that they remained in the pelagic environment throughout their life. Robison and Campbell (1974) suggested a similar mode of life for the paedomorphic Thoracocare (see below).

Potentially, then, progenesis can result in the establishment of phenotypically distinct but genetically similar morphotypes. Slight alteration in the timing of expression of regulatory genes affecting hormonal control of juvenilisation and onset of maturity can result in development of fundamentally different forms. Retention of this regulatory change in future generations would be necessary for the establishment of a separate, viable genotype.

It is tempting to suggest that progenesis, as an evolutionary process in olenellid trilobites, may be one reason for some of the problems encountered in supraspecific classification of Early Cambrian trilobites (Palmer and Halley, 1979). The high degree of morphological plasticity shown may have resulted from weaknesses in the hormonal mechanisms controlling onset of maturity. Clark (1964) noted that paedomorphosis occurred several times during the early history of the Metazoa, suggesting to him that maturation with respect to somatic development was not precisely controlled in these early animals, perhaps because hormonal mechanisms, particularly those controlling growth and reproduction, were relatively imperfect.

Progenesis as an evolutionary process was not restricted only to olenellids among the trilobites.

Robison and Campbell (1974) suggested that the early Middle Cambrian corynexochid Thoracocare evolved by neoteny, probably from an oryctocephalid ancestor. However, although it retained ancestral juvenile characters in the adult, it clearly evolved by progenesis because of its small size and only two thoracic segments. Indeed, the whole order Corynexochida may have arisen by paedomorphosis from a ptychopariid stock (Robison, 1967).

The similarity between Thoracocare and the zacanthoidid Vanuxemella was noted by Robison and Campbell (1974). It is tempting to speculate that zacanthoidids such as Vanuxemella and, to a lesser extent, Albertella and Paralbertella may have arisen by progenesis from a Zacanthoides-like ancestor. Not only do they possess fewer thoracic segments than Zacanthoides (which has nine), but the fewer the thoracic segments (Albertella and Paralbertella each have seven and Vanuxemella has five), the relatively wider the thoracic axes; the more multisegmented the pygidial axes and fewer the pygidial spines; the shorter the eye lobes; the narrower the free cheeks; the shorter the preglabellar areas; and the more divergent the anterior branch of the facial suture.

The British Tremadoc shumariid Acanthopleurella has been interpreted similarly as having arisen by progenesis from a Conophrys-like ancestor (Fortey and Rushton, 1980). The Tremadoc Hospes clonograpti likewise may well be a progenetic conocoryphid.

Evidence has recently been produced (McNamara, 1981) that not only was progenesis an important evolutionary process in Middle Cambrian Xystridurinae in northern Australia, but neoteny was also involved in the evolution of some species of Xystridura. The characteristic morphology of the earliest species of Xystridura, X. negrina, from the early Middle Cambrian Ordian Stage, persisted through a range of species throughout the Ordian and following Templetonian Stages. These structurally ancestral stem forms are characterised by a narrow cranidium; broad cephalic border; anteriorly tapering frontal lobe which reaches the border; anterior two pairs of glabellar furrows which fail to reach the axial furrow; palpebral lobes with poorly defined palpebral furrows set relatively close to the glabella; a broad thoracic axis and well-developed doublure; pygidium with few, generally two to three, axial segments, and well-developed doublure; and a maximum length of about 100 mm.

The small Templetonian xystridurine Galahetes, which reached only about 50 mm in length, possesses adult morphological characteristics found in early to middle meraspid forms of the structurally ancestral xystridurine stem-form and is thought to have arisen by progenesis. Although it also possesses 13 thoracic segments like other xystridurines, the ancestral meraspid Xystridura characters possessed by Galahetes

include a broad cranidium; narrow border; a preglabellar field, as the rounded frontal lobe failed to reach the border; glabellar furrows which all reach the axial furrows; well-defined palpebral lobe set far from the glabella; narrow thoracic axis and no doublure development; and pygidium with six axial rings. All these morphological features occur in the ancestral xystridurine meraspid which was only about 6-7 mm long.

The fact that Galahetes has the same number of thoracic segments as Xystridura suggests that onset of sexual maturity may actually have been triggered by a more rapid production of thoracic segments than occurred in the ancestral xystridurine. Onset of maturity is generally thought to control the number of thoracic segments produced. But, whereas Xystridura does not attain its full complement of thoracic segments and does not become mature until about 15 mm long, maturity and the same complement of segments was attained in Galahetes at a total length of only about 7 mm. This difference suggests that hormonal change affecting earlier onset of maturity may also have affected the more rapid production of thoracic segments. Degree of morphological development between instars, however, remained the same as in its ancestor.

Neoteny also appears to have been an active paedomorphic process in the evolution of some species of Xystridura. The Templetonian X. altera possesses many morphological characteristics of Galahetes and by meraspid of the conservative ancestral stem form. However, it is the largest known xystridurine, as long as to 150 mm. Its slower rate of development is indicated by a cranidium 5.8 mm long in a juvenile, having a degree of morphological development comparable with an ancestral cranidium only 1.5 mm long. It is thought to have reached sexual maturity at a larger size than the ancestral form, but its slower rate of morphological development is attested to by the retention of juvenile characters in its adult stage.

A similar phenomenon, though less pronounced, occurs in X. dunstani. For example, a specimen having a cranidium of the same length as the ancestral form at the onset of maturity has only nine, not 13, thoracic segments, and its morphological characteristics are relatively retarded. The species eventually developed 13 segments but retained juvenile cranidial characters. Thus, whereas morphological development between instars was the same in both the ancestral xystridurine species and Galahetes, the degree of morphological change between instars was reduced in the neotonic X. altera and X. dunstani.

Gould (1977) suggested that progenesis and neoteny may have operate at opposite ends of the  $r - K$  continuum; progenesis will be associated with  $r$  selection and neoteny with  $K$  selection. The progenetic and neotenic xystridurines offer some support for Gould's proposal.

Progenetic forms, such as Galahetes, appear to have been opportunistic species. Galahetes occurs with great frequency at a few localities; a similar situation occurs with the progenetic Olenellus armatus, Acanthopleurella stipulae and, to a lesser extent, species of Thoracocare (T. minuta being locally very abundant, but occurring at nine localities in an area of 2500 km<sup>2</sup> (Robison and Campbell, 1974, p. 278), and T. idahoensis restricted to a single locality)). This occurrence may be a result of their pelagic mode of life. The neotenic X. altera occurs with low frequency locally, perhaps on account of a lower reproductive rate (an aspect of its probably  $K$  strategy). In essence, the benthic environment may have been  $K$  selective, the pelagic environment  $r$  selective, at least for xystridurine trilobites.

Progenesis as an evolutionary process among trilobites seems to have been largely confined to the Cambrian. It is possible that Ordovician and later trilobites may have possessed more efficient hormonal systems for controlling onset of maturity. However, neoteny may well have proved to be a longer lasting evolutionary process in trilobites, and perhaps a more important one in the long term. Whether proparian trilobites evolved by neoteny, as has been suggested by Stubblefield (1960), is still open to debate. However, Clarkson (1975) has produced a persuasive argument that schizochroal eyes evolved from holochroal eyes by paedomorphosis. The smaller number of larger lenses in the schizochroal eye suggests that it arose from the holochroal eye by neoteny. It is noticeable that a number of post-Cambrian trilobite lineages underwent neotenic modification during the terminal parts of their lineages (for example, the reduction and anterior displacement of the eye in phacopids).

Although I do not wish to evoke paedomorphosis as a solution to all evolutionary questions, I believe that in the evolution of Cambrian trilobites, at times it was important in enabling new morphological pathways to become established with a minimum of genetic upheaval.

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### 39. THE LOWER AND MIDDLE CAMBRIAN BOUNDARY IN THE EASTERN BALTIC AREA

By

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Cambrian deposits are widely developed on the northwestern margin of the East European platform, but Cambrian subdivisions are here represented in varying completeness. The most widespread deposits are Lower Cambrian, the Middle Cambrian is not as well represented, and Upper Cambrian deposits are limited.

The Cambrian section of the eastern Baltic area consists mainly of terrigenous rocks, including sandstone, siltstone, and clay. Limestone, in the form of thin interbeds, is known only in the Upper Cambrian, in the most southwestern part of the area.

The main subdivisions (the regional stages) of the eastern Baltic Cambrian are based on acritarch assemblages, because benthic fossils are scarce.

The position of the east Baltic on a platform margin and the occurrence of considerable tectonic movement at the Baikalian-Caledonian boundary have caused not only numerous breaks in sedimentation but also repeated remodelling of the structure of the sedimentation. Only near the Lower and Middle Cambrian boundary has sedimentation been relatively continuous. The boundary beds, determined in the east Baltic as the Aisciai Group, occur as transgressive deposits on rocks of different ages which, in many places, are weathered down to the crystalline basement. The group is thickest (130 m) in the middle of the Baltic syncline.

The section of the Aisciai Group consists of a well-developed transgressive-regressive cycle of deposits. At the initial phase of Aisciaian transgression, comparatively well sorted light oligomictic sandstones and siltstones were deposited. During the following stable phase of transgression, these sediments were overlain by thick strata of interbedded clays and siltstones, including in the middle part some interlayers of oblitic iron ore. Characteristic of this part of the section is the predominance of clays over siltstones and the existence of biostructure of the type of kråksten. The uppermost part of the Aisciai Group is sandstone and siltstone containing thin clay bands. In this part of the section, considered by us as deposits of the regressive phase, bioturbated kråksten are absent, and the deposits are characterized by horizontal bedding. Accumulations of glauconite and valves of inarticulate

brachiopods may be observed on the bedding planes. Frequently these planes are also marked by conglomerate lenses consisting of phosphatic pebbles.

The Aisciaian rocks are subdivided into three regional stages, which are, in ascending order: Vergale, Rausve, and Kibartai. The lowermost part of the sequence, tentatively considered here as a part of the Vergale Stage due to its sandy deposits, contains rare acritarchs, whose possible significance as an independent assemblage of the stage level is not yet clear. The Vergale and Rausve Stages are classified as belonging to the Lower Cambrian, whereas the Kibartai Stage is referred to the Middle Cambrian. Here, as in all of the whole territory of the U.S.S.R. and the neighboring countries of Scandinavia and western Europe, the boundary between the Lower and Middle Cambrian is placed by the appearance of representatives of the family Paradoxididae or its accompanying forms. Stages of the East Baltic Cambrian may be correlated with the Scandinavian trilobite zones on the basis of rare trilobites and inarticulate brachiopods.

The Vergale Stage, according to finds of Strenueva primaeva (Brøgger), belongs to the upper part of the Holmia Stage (Holmia kjerulfi Zone), whereas the lower part of the Holmia Stage corresponds to the underlying Liivian Stage, as judged by the occurrence of Schmidtellus mickwitzii (Schmidt).

No trilobites have been found as yet in the Rausve Stage. Based on the acritarch correlation with the section of the platform part of Poland, where the corresponding beds contain trilobites of the Protolenus Stage, the Rausve Stage is treated as a stratigraphic equivalent of the corresponding stage.

The Kibartai Stage, containing Ellipsocephalus puschi Orłowski, E. polytomus Linnarson, Strenuella (Comluella) samsonowiczi Orłowski, S. (C.) insolita N. Tchern., and Lingulella ferruginea Salter, correlates with the Eccaparadoxides oelandicus Stage.

The coincidence of the boundaries of the temporal changes in trilobite fauna with the stages of sedimentary development, found in the east Baltic Cambrian section, can also be observed in other regions of the western margin of the platform (Ukraine, Byelorussia, and Poland).

Consequently, the shift of crucial moments in the trilobite evolution and succession of the sedimentation, caused mainly by local tectonic factors, may be considered as a characteristic feature of Early and Middle Cambrian time for the whole western region of the East European platform.

#### 40. SEDIMENTOLOGICAL CHARACTERIZATION OF THE BOUNDARIES BETWEEN THE LOWER CAMBRIAN STAGES IN THE EASTERN BALTIC AREA

By

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The existence of exposures, numerous borings, and a long history of investigation of the east Baltic makes the Lower Cambrian sequence of this area a standard for the whole eastern European platform. For this reason, determination of the character and changes taking place during deposition of the first half of the Lower Cambrian are of great interest from the stratigraphical point of view, especially for drawing boundaries of subdivisions.

The Lower Cambrian is represented in the East Baltic area only by marine terrigenous rocks. The main part of these sedimentary rocks is composed of siltstones and claystones. In the geological history of the Early Cambrian sedimentation, three stages may be rather clearly distinguished: Baltian, Liivian, and Aisciaian (part). The first two belong entirely to the Lower Cambrian, but the upper beds of the third, the Aisciaian Stage, belong to the lower part of the Middle Cambrian. Deposits of different stages vary generally in accordance with the tectonic plan of the region, causing considerable differences in the distribution of sediments. Also, the changes in the sedimentary conditions are not very traceable.

A complete transgression-regression cycle of sedimentation can be observed in the structure of the Baltian and Aisciai Groups; the cycle is less clearly traceable in the section of the Liivian Stage.

Typical of the mineral composition of Cambrian deposits in the studied area is the weak alternation during post-depositional diagenesis (in katagenetic phase). We used the mineral association to reconstruct environmental conditions and to study the peculiarities of the sedimentary process at this interesting stage of the Earth's history.

The analysis of the sediments indicated that the principal source area for this material was covered by older sedimentary rocks. Only the mineral composition of the Baltian rocks indicate that the material was derived directly from the crystalline basement. The mineralogical analysis of clastic material indicated some local synsedimentary tectonic structures in the basin of sedimentation, too. The regular increase of stable minerals in the clastic component upward in the section gives evidence of a repeated redeposition of the sedimentary material and reduction of the influence of the crystalline

basement. Some changes in the composition of the mineral association helped to identify the direction of sediment transport and other characteristic features of the lithofacies and paleogeography.

The clay-mineral composition and distribution also indicates an intensive denudation of earlier sedimentary rocks during the Early Cambrian. The lateral distribution of clay mineral associations shows a clearly expressed zonality in the basins, especially in their shallow sea belt. The chemical diagenesis of clay minerals into mixed-layer clay minerals is not typical of Lower Cambrian sediments. It marks mainly the interval of intensive accumulation of ferruginous compounds (oblitic iron ore) in the middle of the Aisciaian Stage. Most important among them is periodic short-term lasting decrease of salinity. This phenomenon reflects the influence of the consistent humid climate in the surrounding area. One of these periods of water freshening is marked by interbeds of ferrous oblitites that have a characteristic lateral zonality of goethite-chamostite-siderite minerals.

In accordance with these data, it is of special interest to know what events occurred at the two supposed alternatives of the Precambrian-Cambrian boundary, at the base and top of the Baltic Group. More significant changes in hydrochemical conditions of sedimentation took place in the east Baltic region at the base of the Baltic Group. These changes coincide with the appearance of *Sabellidites* and were taken by the authors as indicating the lower boundary of the Cambrian. The underlying strata of the upper Vendian, judging by the wide distribution of kaolinite, siderite, and hematite and the lack of glauconite and phosphate, were formed in a greatly freshened basin of the humid type. This basin type is confirmed also by the occurrence of organic remains in the upper Valdai Group, remnants of algae and diverse microphytoplankton. In the Baltian deposits, skeletal fauna and numerous traces of mud-eaters immediately appear with the beginning, whereas remains of algae completely disappear. Besides, it must be noted that the structural plan of sedimentation is similar in both subdivisions, even where a hiatus was observed between them. The transgression entered the studied area from the east, from the direction of the

Moscovian syncline. Sedimentological features of the upper Vendian and Baltian deposits do not show any remarkable changes in climate. Both subdivisions, where together, are composed of terrigenous sediments of humid climatic conditions. Carbonate sediments are lacking.

The boundary between the Baltian and Liivian Groups, that is, between pre-trilobite beds and trilobite-bearing beds, is characterized by a great remodelling of the structural plan of sedimentation, accompanied by breaks in the sedimentation process. But, at this time, the hydrochemical regime of the basin, humid normal-marine type, was completely

preserved. This preservation is indicated by the wide distribution of glauconite and phosphate in Liivian deposits, too. These environmental conditions, with slight fluctuations, lasted during the entire Liivian and Aisciaian Stages and a significant change occurred only in post-Aisciaian, Middle Cambrian time. In the strata overlying the Aisciai Group, the glauconite-phosphate mineral association is lacking. Interbeds of dark shale (alum shale) and carbonate rocks appear. Those changes indicate a drying of the climate in the second half of the Middle Cambrian, and this condition was typical during the rest of the lower Paleozoic in the eastern Baltic region.

## 41. PALEOZOOGEOGRAPHY AND BIOSTRATIGRAPHY OF UPPER CAMBRIAN AND TREMADOCIAN CONODONTS

By

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Trilobites, graptolites, and conodonts are the main fossils used for correlating Upper Cambrian and Tremadocian strata. The distribution of trilobites, graptolites, and upper Tremadocian conodonts has been much discussed in the literature. However, conodonts from the Croixian Series (Upper Cambrian) and the lower part of the Tremadocian Series and their equivalents have been known only for a short time (Müller, 1959; Miller, 1969), thus distribution of these faunas is still incompletely known. As more data become available, distribution patterns begin to emerge which clarify conodont biostratigraphy of these strata.

### PALEOZOOGEOGRAPHY OF CONODONT LINEAGES

Croixian and Tremadocian conodonts can be divided into several evolutionary lineages, which have nonuniform ranges in different parts of the world. A fundamental division of these faunas is between the Order Paraconodontida and the Order Conodontophorida. Within the latter group, also called euconodonts, several evolutionary lineages existed during the Croixian and Tremadocian. The distribution of these lineages is not uniform in time or space, although some taxa are restricted in one or both parameters. Biostratigraphic schemes depend on temporal restriction of taxa, and the geographic applicability of these schemes depends on spatial distribution of the taxa.

#### Paraconodont lineage

Many of the Croixian and Tremadocian paraconodonts were described by Müller (1959), although additional species have been described subsequently by others. Little biostratigraphic use has been made of paraconodonts, partly because of a general lack of sequential collections. The potential of paraconodonts for biostratigraphy seems to be limited by the long range of many taxa and by the variable occurrence of paraconodonts in general.

Upper Cambrian paraconodonts were adapted to warm, low-latitude environments in areas such as North America and Australia, and to cold, high-latitude environments in areas such as northern Europe. Euconodonts seem to have developed in warm, low-latitude environments near the end of the Franconian Stage, and there they quickly dominated over the paraconodonts. In the cold environment of Sweden and Poland, paraconodonts continued a dominant role until nearly the start of the Tremadocian, when more advanced euconodonts evolved and adapted to the cold environments. Some paraconodonts persisted well into the Tremadocian in both warm and cold areas.

#### Euconodont lineages

Among Croixian and Tremadocian euconodonts, Miller (1980) recognized two major evolutionary lineages and possibly a third. The Proconodontus lineage is a primitive euconodont stock which developed during the Upper Cambrian Franconian Stage and persisted well into the Ordovician. Proconodontus apparently developed from a paraconodont stock in warm, low-latitude, cratonic environments. A sequence of several species is known from North America and Australia, and some species are known from Iran (Müller, 1973) and China (An and Yang, 1980). Euconodontus is a descendant of Proconodontus, which is more widespread, being reported from North America, Australia, China, Korea, Siberia, Iran, and Turkey. Cambrooistodus evolved from Euconodontus, but it is apparently endemic to North America. In North American shallow marine environments Proconodontus and Cambrooistodus abruptly became extinct at the top of the Proconodontus Zone, but the former has been reported from younger strata in several other areas. Euconodontus survived and, immediately after the extinction of the other two genera, of the other two genera, rise to Cordylodus just before the start of the Tremadocian. Cordylodus evolved into a series of species, many of which are cosmopolitan. Because of their wide distribution and rapid evolution, elements of the Proconodontus lineage are useful for both regional and intercontinental correlation.

The Teridontus lineage is a second euconodont stock, which is clearly not related to the Proconodontus lineage, but its ancestry is uncertain. In Australia and China the ancestral form, Teridontus nakamurai, is found in upper Franconian, Trempealeuan, and Tremadocian equivalents. In shallow marine deposits from North America, the species is absent from most of the Croixian except for two occurrences near the base of the Trempealeuan in Texas. Following the latest Croixian extinction among the Proconodontus lineage, T. nakamurai migrated rapidly with Cordylodus proavus and became cosmopolitan. The former species occurs in strata of latest Croixian and early Tremadocian age. It dominates North American shallow marine faunas and also occurs in deeper facies.

Beginning in latest Croixian time the Teridontus lineage diversified rapidly following a long period of little or no evolution. This lineage has two branches. The older branch consists of the unusually ornamented genera Hirsutodontus and Clavohamulus. Species of Hirsutodontus occur in shallow marine deposits of latest Croixian and early Tremadocian age. Hirsutodontus occurs in North America, Australia, and Siberia. Clavohamulus occurs mostly in North American shallow marine deposits, but one species occurs only in Siberia. Species of these genera are used for biostratigraphy in North America, and some are useful for intercontinental correlation.

The other branch of the Teridontus lineage consists of costate simple-cone genera. Included here are important Tremadocian and Arenigian genera, including Semiacontiodus, Acontiodus (some form-species), Utahconus, Monocostodus, Scolopodus, some form-species of Drepanodus, and probably others. The first four genera are found mostly in lower Tremadocian strata, but such form-species as Acontiodus iowensis, A. propinquus, and A. staufferi continue into the upper Tremadocian. These four genera are found mostly in shallow marine deposits in North America, Australia, and China. Semiacontiodus is also known from Siberia, and Utahconus also occurs in Turkey. Scolopodus and Drepanodus are also widespread. Because of their wide distribution, all of these genera are useful for regional and intercontinental correlation of warm-water shallow marine Tremadocian deposits.

The third lineage of Tremadocian conodonts consists of a single genus, Fryxellodontus. This complex euconodont apparatus represents either an offshoot from Proconodontus or a completely separate conodont stock of unknown origin. Fryxellodontus is widespread in lower Tremadocian shallow marine deposits in North America, and two specimens have been reported from strata of similar facies and age in Australia. There are no certain descendants of the genus. Because of its distribution and short stratigraphic range, the genus is useful for correlation

within North America. It also provides a useful correlation to Australia.

#### Paleozoogeography

One of the most striking aspects of the distribution of Ordovician conodonts is the contrast between the North Atlantic Province (northern Europe and eastern North America) and the North American Midcontinent Province (central and western North America). This contrast first developed during the Late Cambrian between paraconodont faunas in northern Europe and Proconodontus-lineage faunas in North America. Water temperature appears to be one of the most important factors controlling distribution. By early Tremadocian time, Midcontinent Province faunas consisted of many genera from three lineages, and rather diverse faunas are known from warm-water deposits of several continents.

By early Tremadocian time, faunas from the North Atlantic Province and other cold-water environments were dominated by euconodonts, such as Eoconodontus, Cordylodus, and Teridontus, instead of by paraconodonts. Such low-diversity faunas are known from Oaxaca, Mexico (Robison and Pantoja-Alor, 1968; Miller, Robison, and Clark, 1974), northwestern Canada (Landing, Ludvigsen, and von Bitter, 1980), and Scandinavia (J. F. Miller, unpublished data). In Iran similar faunas also contain two species of Proconodontus and several paraconodonts not usually found in Tremadocian strata (Müller, 1973).

Rapid evolution of the cosmopolitan genus Cordylodus provides a basis for correlating strata from the two faunal provinces. By late Tremadocian time, North Atlantic Province faunas were much more diverse, but the contrast with the American Midcontinent Province was more pronounced. Correlation of upper Tremadocian strata between the two provinces is difficult because the evolution of Cordylodus slowed, and the genus is usually absent from uppermost Tremadocian strata.

#### BIOSTRATIGRAPHY

Correlation of Croixian and Tremadocian conodont zonal schemes from different environments is shown on figure 1. The sections from the U.S.A., Australia, North China, and Siberia are from low-latitude, warm platform environments. The sections from Iran and Scandinavia are from high-latitude, cold, platform environments. The Canadian section is from an uncertain facies, but it is from a continental margin environment, which was probably relatively cool and deep.

TEXAS, USA		AUSTRALIA		NORTH CHINA		SIBERIA, USSR		NW CANADA		IRAN		SCANDINAVIA							
CANADIAN	Fauna C	---	---	?	?		Assemblage 2				← Zone 7 (1)	UPPER TREMADOCIAN							
		<i>Cordylodus angulatus</i>	<i>C. rotundatus-C. angulatus</i> Zone		WARENDIAN	<i>Acanthodus costatus-</i>  <i>"Acodus" oneotensis</i>  Zone	---	?	---	← Zone 6 (2)	← Zone 5 (1)								
			D90	<i>C. caseyi</i> Sz.															
	<i>Cordylodus lindstromi</i>	<i>C. prion</i> Sz.		DATSONIAN	Zone	LOWER ORDOVICIAN	---	---	Fauna B ?	---	---	LOWER							
		D75	<i>C. lindstromi</i> Subzone																
	<i>Cordylodus proavus</i> Zone	<i>Clavohamulus hintzei</i> Sz.	<i>Cordylodus oklahomensis</i> Subzone		Drepanodus simplex Zone	---	---	Assemblage 1	---	---	---	---	---						
			<i>Hirsutodontus simplex</i> Sz.																
		<i>Clavohamulus elongatus</i> Sz.	<i>O. bicuspatus-D. simplex</i> Zone		<i>Cordylodus proavus</i> Zone	---	---	---	---	---	---	---	---						
		D59																	
		D53	<i>Cordylodus proavus</i> Zone																
<i>Hirsutodontus hirsutus</i> Sz.	<i>Hirsutodontus hirsutus</i> Zone		UPPER CAMBRIAN	Zone	---	---	---	---	---	---	---								
D37																			
TREMPEALEAUAN	<i>Proconodontus</i> Zone	<i>Cambroostodus minutus</i> Sz.	B71 PAYNTONIAN		<i>Proconodontus</i> Zone	---	---	---	---	---	---	---							
		<i>Eoconodontus notchpeakensis</i> Subzone	---										---	---	---	---	---	---	---
		<i>Proconodontus muelleri</i> Sz.	PRE-PAYNTONIAN																
	<i>Proconodontus posterocostatus</i> Subzone	B33 A		---	---	---	---	---	---	---	---	---							
	<i>Proconodontus tenuiserratus</i> Zone	B20 PRE-PAYNTONIAN																	
	<i>Proconodontus tenuiserratus</i> Zone	B4 POST-IDEAMEAN		FRANCONIAN	Zone	---	---	---	---	---	---	---	---						
No Zonation																			

Figure 1.--Worldwide correlation of conodont zones from diverse environments. Zones have not been proposed for most of the Scandinavian section. For Australian section, numbers indicate trough samples of Druce and Jones (1971) which mark zone boundaries; B4-B71 are from Black Mountain section, and D34-D90 are from Mt. Datson section. For Iranian section the number of samples defining each zone is shown in parentheses. Depositional environments and sources of data discussed in text.

The zonal scheme for Texas is modified from Miller (1980). The Australian section is a composite of two sections from Druce and Jones (1971). It is partly based on additional personal collections and on reidentification of some pre-Payntonian Stage faunas by Druce (personal commun.). Payntonian and older strata are from the Black Mountain section; younger strata are from the Mt. Datson section. The Siberian section is from Abaimova (1972). Correlation of the North China section is slightly revised from An and Yang (1980). The Canadian section is based on Landing, Ludvigsen, and von Bitter (1980). The section from Iran (Müller, 1973) is a composite of several sections. The correlation of zones 1 and 2 is very uncertain. Zones 5-7 are based on only 4 samples, and the approximate level of these samples is shown by arrows. The Scandinavian section is based on personal collections. Control on the Olenid-Tremadocian boundary is from Naersnes, near Oslo, Norway. Control on the lower-upper Tremadocian boundary is from conodonts from glauconite sands near the base of the Ceratopyge limestone at Stora Bakor, Sweden.

#### CONCLUSIONS

There is considerable variation in Upper Cambrian and Tremadocian conodont faunas. Water temperature appears to have been a major factor controlling variation. Cold-water faunas are of low diversity and have more abundant paraconodonts; euconodonts appeared earlier in warm-water environments and achieved greater diversity. Excellent correlation is possible among several warm-water cratonal sequences. Correlation with strata from cold environments is less detailed but still possible by utilizing cosmopolitan euconodonts. Correlation will doubtless improve as more data become available.

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## 42. UPPER CAMBRIAN FAUNAL DISTRIBUTION IN SOUTHEASTERN CALIFORNIA AND SOUTHERN NEVADA

By

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Abundant Middle and Upper Cambrian fossils from the southern Great Basin are restricted to a few thin stratigraphic intervals of limy carbonate and fine-grained terrigenous clastics within thick unfossiliferous sequences of light- to dark-gray carbonates of the Carrara, Bonanza King, and Nopah Formations. The couplet comprising the Dunderberg Shale and Halfpint Members of the Nopah Formation is one of these fossiliferous intervals. This report summarizes the paleontological data from sections in southern Nevada and southeastern California (fig. 1). Another report (Cooper and others, this volume) summarizes the depositional environments for the same sections.

Trilobites, inarticulate brachiopods, conodonts, sponge spicules, gastropod steinkerns, and pelmatozoan (eocrinoid) debris are common in most sections. Taxa characteristic of the trilobite zones of the Pterocephaliid bioterm of Palmer (1965), and the *Anqulotreta missouriensis*, *Apotreta expansa*, and *Linnarssonella* brachiopod zones (Bell and Ellinwood, 1962, Kurtz, 1971) indicate that the rocks are of medial Late Cambrian (Dresbachian to Franconian) age and are temporally equivalent to other sections in Nevada and Utah (Palmer 1965; Cook and Taylor, 1975; Koepnick, 1976; Rowell and Brady, 1976). Detailed analyses of lithofacies and fossils within this time framework indicate the existence of a variety of platform-margin, shallow-shelf, and outer shelf paleoenvironments.

The orange-brown weathered carbonate and shale interval represented by the Dunderberg Shale and Halfpint Members is distinct from the thick-bedded carbonates of the Bonanza King Formation. The basal contact is either an abrupt lithologic change from carbonate to shale or, in some sections, it may be gradational, recognized by the first occurrence of bioclastic calcarenite. Trilobite distribution indicates that the base of the Dunderberg is diachronous (fig. 2), but physical evidence of a hiatus between the Bonanza King and the Dunderberg is not evident in any

of our sections. Contact with the overlying Smoky Member is defined at the base of the first light- or dark-gray, weathered, thickly bedded, vuggy dolostone. The Smoky is generally devoid of macrofossils, although in sections near the southeast edge of the study area oncolites and other cryptalgal structures are common. In all sections the contact is conformable.

### PALEONTOLOGY

Of the 30 sections studied (fig. 1), we have chosen to summarize the paleontological data from a representative sample of 12 sections (fig. 2) that trend approximately normal to depositional strike. Distribution of fossils and lithosomes indicates that outer shelf paleoenvironments existed towards the northwest, and shallow lagoons, shoals, and banks existed towards the southeast (Sundberg and others, 1979; Cooper and others, this volume). The diversity and abundance of taxa is greatest within the carbonate interbeds of the Dunderberg Member (lagoons, subtidal shelf, oolite shoals) and in pelmatozoan calcarenites (packstone and wackestone) within the Halfpint Member. Other lithosomes contain fewer fossils, and the crinkly cryptalgal and thrombolitic beds (algal banks) lack macrofossils, but may contain conodonts.

#### Trilobites.

Trilobite zones for Upper Cambrian rocks of the Great Basin were proposed by Palmer (1965). Although he did not have measured sections from the southern part of the region, scattered collections provided sketchy information. Our collections support the succession of assemblage zones he reported (fig. 2), although the apparent diachroniety at the base of the sections suggest some revisions may be necessary. We have identified 36 species from 17 genera, including five new species. The trilobite species are dominated by two agnostid families, Agnostidae and

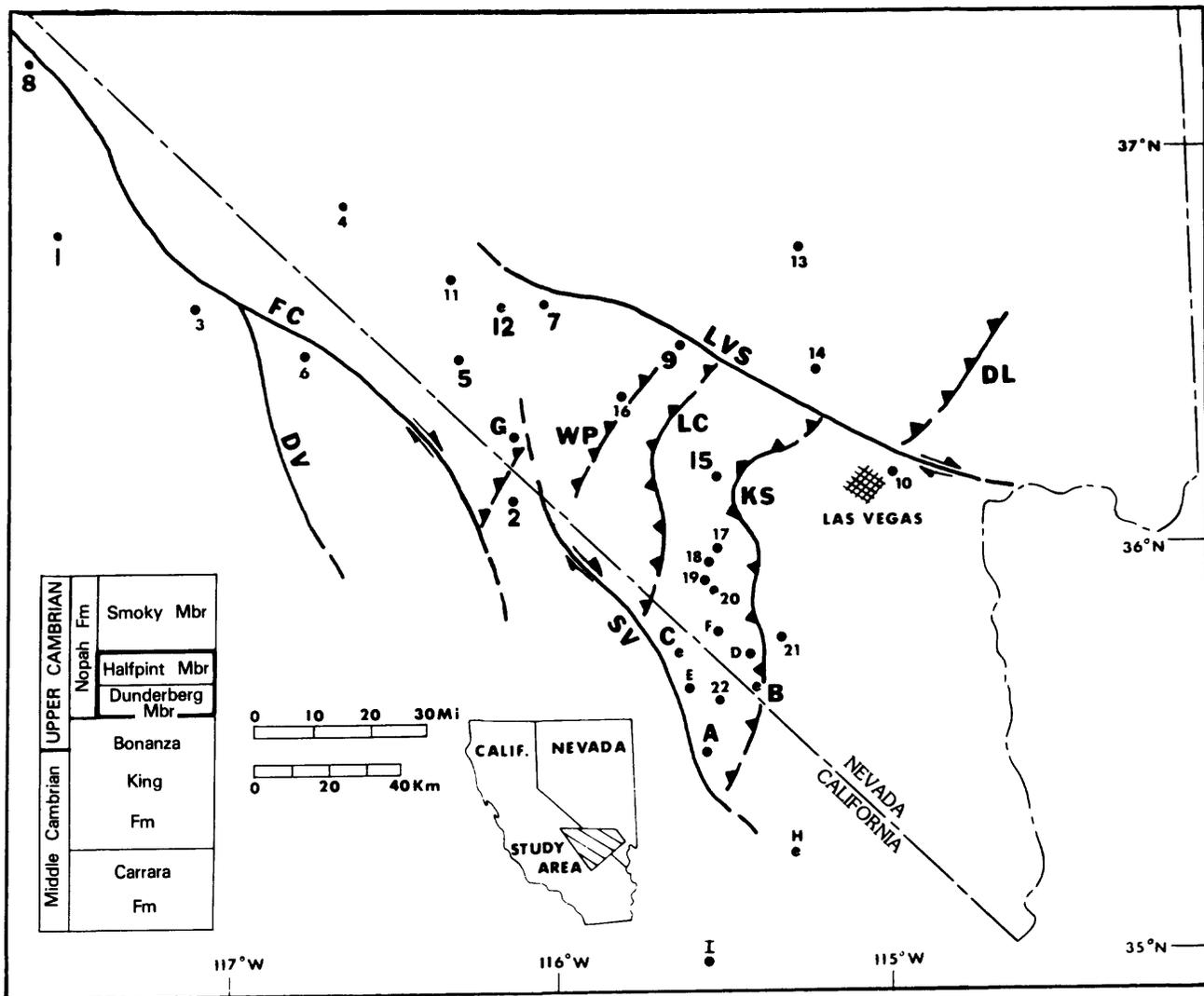


Figure 1.--Location of studied sections of the Dunderberg Shale and Halfpint Members of the Nopah Formation in the southern Great Basin. Sections described in the text (reference sections) are indicated by larger numbers and letters. Major faults (dashed where approximately located) in the area are indicated as follows: FC, Furnace Creek fault; DV, Death Valley fault; SV, Stewart Valley fault; LVS, Las Vegas shear zone; WP, Wheeler Pass thrust fault; LC, Lee Canyon thrust fault; KS, Keystone thrust fault; DL, Dry Lake thrust fault. Sawteeth on upper plate of thrust faults. The lower part of the Carrara is Early Cambrian and the upper parts of the Nopah is Early Ordovician.

Pseudagnostidae, and by three nonagnostid subfamilies, Elviniidae, Aphelaspidae, and Pterocephaliidae.

The *Aphelaspis?* Zone is tentatively recognized (secs. 5, 7, and 9) on the basis of *Aphelaspis haquei* and *Blountia bristolensis*. The *Dicanthopyge* Biozone contains *Aphelaspis subditus*, *Dicanthopyge convergens*, *D. quadrata*, *Dunderbergia brevispina?*, *Prehousia prima*, and *Pseudagnostus communis*. *Prehousia* Zone taxa include *Cernuolimbus laevifrons*, *Homagnostus obesus*, *Prehousia alata?*, *P. identa*, and

*Pseudagnostus communis*. The lower *Dunderbergia* Zone is characterized by *Cernuolimbus granulosus*, *C. laevifrons*, *Dunderbergia? anyta*, *D. nitida*, *Elburgia granulosa*, *E. intermedia*, *Homagnostus tumidosus*, *Minupeltis conservator*, *Prehousia diverta*, *Pterocephalia concava*, *Sigmocheilus notha*, *Strigambitus transversus*, and *S. utahensis*. The upper *Dunderbergia* Zone is characterized by *Apachia butlerensis*, *A. prima*, *Cernuolimbus* cf. *C. depressus*, *Dunderbergia polybothra*, *D. varigranula*, *Elburgia*

TRILOBITES	BRACHS	SECTIONS														
		8	1	5	12	G	7	9	2	C	15	A	B			
ELVINIA	LINNARS-SONELLA	█	█	█	█	█	█	█	█	█	█	█	█	█	█	█
Upper DUNDERBERGIA	APSOTRETA	█	█	█	█	█	█	█	█	█	█	█	█	█	█	█
Lower DUNDERBERGIA	EXPANSA	█	█	█	█	█	█	█	█	█	█	█	█	█	█	█
PREHOUSIA	ANGULOTRETA	█	█	█	█	█	█	█	█	█	█	█	█	█	█	█
DICANTHOPYGE	MISSOURIENSIS	█	█	█	█	█	█	█	█	█	█	█	█	█	█	█
APHELASPIS?	? ? ?	█	█	█	█	█	█	█	█	█	█	█	█	█	█	█

Figure 2.--Age range of 12 sections of Dunderberg Shale and Halfpint Members, Southern Great Basin, Nevada-California, based upon trilobite zones and inarticulate brachiopod zones. Open rectangles indicate approximate age, reflecting poorly preserved and (or) nondiagnostic taxa.

Nogamiconus cambricus, Proconodontus muelleri, Proconodontus sp. A, Prooneotodus gallatini, P. rotundatus, P. tenuis, P. n. sp. A, Prosagittodontus dunderbergiae, P. eureka, Westergaardodina bicuspidata, W. moessebergensis, and genus and species indet. Specimens of Furnishina asymmetrica and Hertzina? sp. reported by Miller and Paden (1976) are considered Furnishina furnishi and Prooneotodus tenuis, respectively.

The conodont taxa are stratigraphically long ranging and are not presently useful for precise biostratigraphic zonation of these Upper Cambrian rocks. The most abundant taxon is the protoconodont Prooneotodus tenuis (Müller), which comprises about 70 percent of the specimens. Conodonts were recovered from all reference sections and are most abundant in the lower and upper Dunderbergia Zone. Samples containing the highest diversity and abundance are the carbonates within the Dunderberg Shale Member, especially those in the central part of the study area representing the oolite shoal (secs. 5, 7, 12, and G). Lowest diversity occurs towards the southeast (secs. 15, A, B, and C), and sections H and I were barren. This distribution indicates that the protoconodont- and paraconodont-bearing organisms existed in a variety of shallow, normal-marine to possibly restricted platform-margin and shelf paleoenvironments. Except for occurrences of P. tenuis, conodonts are absent below the lower Dunderbergia Zone, although the distribution of lithofacies indicates that suitable environments existed in the area during the time of deposition of strata containing the Aphelaspis, Dicanthopyge, and Prehousia Zones. This evidence suggests that the protoconodont-bearing animal had slightly different environmental tolerances than the paraconodont-bearing animal.

quinnensis, Morosa extensa, Pseudagnostus leptogranulata, Pterocephalia elongata, P. santisabae, Sigmocheilus grata, and Strigambitus? blepharina. Elvinia Zone taxa include Dunderbergia nitida, Elvinia roemeri, and Pterocephalia sanctisabae.

Two aspects of the trilobite distribution are significant: (1) At the species level there is considerable variation among sections, and considering our relatively thorough sampling, this variation reflects local changes in paleoenvironments. For example, comparison of taxa from sections 5, 7, 12, and G (fig. 1) indicates that less than 50 percent of the species are common to all four sections. (2) The trilobites represent "onshore" taxa of Taylor (1977), but in our sections, further refinement is possible. Species of Aphelaspidae occur more commonly in the oolite shoal and subtidal shelf, and species of Elviniidae and Pterocephaliidae occur in shallow subtidal and lagoonal as well as oolite shoal and subtidal paleoenvironments. The agnostids occur in the subtidal shelf, outer shelf, and oolite shoals.

#### Conodonts.

Upper Cambrian conodonts from rocks in the Great Basin have been described by Müller (1959), Miller (1969), Miller and Paden (1976), and Miller and others (1981). Sixteen single element form species of paraconodonts and one form species of protoconodont, including three new species, occur in our sections. These taxa include Distacodus? palmeri, Furnishina furnishi, F. n. sp. A, Muellerodus pomeranensis,

#### Brachiopods.

Abundant and relatively diverse inarticulate brachiopods have been reported from Upper Cambrian rocks of the southern Great Basin, but little taxonomic information has been published (Rowell and Brady, 1976; Rowell and Henderson, 1978). Eleven species occur in our sections: four species of Lingulida and seven species of Acrotretida. These taxa are biostratigraphically significant (Miller and others, 1981) and in general parallel the brachiopod biozones developed for platform sequences in the midcontinent region by Bell and Ellinwood (1962) and Kurtz (1971).

Species occurring in the Angulotreta missouriensis Zone include A. missouriensis?, A. triangularis, Apsotreta sp., Physotreta? sp., Lingulella sp. A, and L. sp. B. Taxa found in the overlying Apsotreta expansa Biozone include Angulotreta? catheta, Apsotreta expansa, Lingulella oweni, Lingulella sp. A, and L. sp. B. Species in the overlying Linnarssonella Zone include L. girtyi, Lingulella sp. B, and Tropidoglossa modesta.

Inarticulate brachiopod zones can be correlated with trilobite zones from the Great Basin (fig. 2); however, temporal relationships are somewhat imprecise (Rowell and Brady, 1976). Difficulties stem from the lack of formal brachiopod zones from the Great Basin, and arise because taxa from platform sequences in the midcontinent are less diverse than those of the shelf and platform-margin sequences.

Distribution of brachiopods in our sections parallels that of the trilobites and conodonts. The greatest diversity and abundance occurs in the Dunderberg carbonates, especially in the central part of the study area (secs. 5, 7, 12, and G). Specimens are most abundant within the lower and upper Dunderbergia Zones. Rowell and Brady (1976) indicated that brachiopod abundance and diversity in western Utah and eastern Nevada is greatest in open marine, shallow shelf paleoenvironments and lowest in shoal, lagoonal and peritidal paleoenvironments. Similar patterns of distribution appear to continue southwestward along strike from Nevada and Utah into eastern California.

#### Parazoa

Two types of sponge spicules occur in our sections and have been assigned to the genera Chancelloria and Hintzespongia. Chancelloria occurs in rocks containing trilobites of the Dicanthopyge, Prehousia, and lowest part of the lower Dunderbergia Zones. Hintzespongia rarely occurs below the base of the lower Dunderbergia Zone and is present up into the Elvinia Zone. This distribution suggests that these sponge genera may provide limited, but useful biostratigraphic control. Distribution of the spicules closely parallels that of the trilobites and the inarticulate brachiopods.

#### PALEONTOLOGICAL INTERPRETATIONS

The Cambrian taxa provide detailed biostratigraphic information used in establishing time lines among the sections, and for correlation with miogeoclinal rocks in the central Great Basin; less detailed correlations can be made with platform rocks exposed in the midcontinent. As indicated in figure 2, the base of our sections appears diachronous when compared with the trilobite zones established by Palmer (1965). This apparent diachroneity, coupled with the absence of physical evidence for unconformities, suggests that as presently defined the trilobite-assemblage zones may not be good chronostratigraphic markers.

Lateral and vertical changes in lithosomes within these middle Upper Cambrian rocks indicate the existence of complex local paleoenvironments (Cooper and others, this volume). Distribution of taxa within

these lithosomes illustrates the presence of two facies-controlled benthic associations. One is represented by trilobites, brachiopods and sponges, and the other is predominantly eocrinoidal. Mixing of these two associations, represented commonly by the pelmatozoan calcarenite lithofacies and some eocrinoidal debris in the carbonates of the Dunderberg Shale Member, was primarily due to storm transport. Occurrence of conodonts with both of these benthic associations and within the cryptalgal lithofacies indicates the conodont-bearing organisms were less facies dependent and may have had a nektic habitat. Except for scattered trilobites and inarticulate brachiopods, the shale lithofacies and siltstone lithofacies contain few fossils, indicating that unsuitable living conditions existed during episodic influxes of the fine-grained terrigenous sediment.

Acknowledgments: Part of our research (including Cooper and others, this volume) was supported by a grant from the American Chemical Society, Petroleum Research Fund to Miller and Cooper. We wish to thank the many undergraduate and graduate students who provided field and laboratory assistance from 1975 to 1980.

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### 43. GRAND CYCLE A (LOWER CAMBRIAN) OF THE SOUTHERN GREAT BASIN: A PRODUCT OF DIFFERENTIAL RATES OF RELATIVE SEA-LEVEL RISE

By

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The concept of grand cycles was established by Aitken (1966) for Middle Cambrian to Middle Ordovician sediments of the Canadian Rockies of Alberta. Fritz (1975) extended the grand cycle concept into the Lower Cambrian throughout the Cordillera from the Yukon to northern Mexico. Based on trilobite biostratigraphy, Fritz defined three Lower Cambrian grand cycles, which he called A, B, and C. The basal cycle, grand cycle A, is particularly well exposed in the White-Inyo Mountains and Death Valley area of eastern California and in adjacent Esmeralda County of Nevada. In this report we summarize the depositional evolution of grand cycle A in this region and postulate a mechanism for its development.

#### ENVIRONMENTAL STRATIGRAPHY

Grand cycles are couplets that consist of a basal, terrigenous clastic half-cycle gradationally overlain by a carbonate half-cycle. The stratigraphic units of grand cycle A in the southern Great Basin are shown in Figure 1.

#### Terrigenous Clastic Half-Cycle

The terrigenous clastic half-cycle is represented in the White-Inyo Mountains by the quartzites and siltstones of the Campito Formation, and in the Death Valley area by siltstones, sandstones and conglomerates of the upper lower member, middle member, and lower upper member of the Wood Canyon Formation. Recently completed studies of the Campito Formation by Mount (1980) and the Wood Canyon Formation by Diehl (1979) permit a reconstruction of the depositional environments in which these sediments accumulated.

During deposition of the lower part of grand cycle A, the cratonward Death Valley area, as interpreted by Diehl, was the site of a complex mosaic of peritidal and alluvial environments (fig. 2A). Depositional episodes within this area were more strongly controlled by local tectonism than in the White-Inyo facies; this is reflected in the fact that the member boundaries in the Wood Canyon do not coincide with grand cycle boundaries.

In the White-Inyo Mountains the base of the Campito Formation (and the base of grand cycle A) is sharp and erosive. Mount (1980) has described evidence for subaerial erosion of the top of the underlying Deep Spring Formation. The siliciclastic deposits (Andrews Mountain Member of the Campito Formation) that directly overlie this unconformity consist of hummocky, cross-stratified, heterolithic deposits indicative of offshore, shallow-shelf deposition. The beginning of grand cycle A deposition was evidently accompanied by a rapid deepening of the sea, because no facies are preserved that reflect a transition between the erosive, emergent conditions of the underlying Deep Spring Formation carbonates and the nonerosive, deeper water conditions of the Campito Formation.

Throughout most of the deposition of the terrigenous clastic half-cycle of grand cycle A, the White-Inyo Mountains area was an offshore, shallow-shelf environment where deposition was controlled by intermittent, catastrophic storms (fig. 2A). It is thought that storm-surge ebb flows transported sediment seaward across the shelf (Mount, 1980).

#### Transitional Deposition

The terrigenous clastic half-cycle of a grand cycle is gradationally overlain by a carbonate half-cycle. In the White-Inyo Mountains the transition between the two half-cycles of grand cycle A is represented by the sandstones, shales, and archeocyathid bioherms of the upper parts of the Montenegro Member of the Campito Formation. Mount (1980) has suggested that these strata reflect low-energy, subtidal to intertidal depositional environments. In the Death Valley area the correlative lower part of the upper member of the Wood Canyon Formation contains sandstones and siltstones interpreted by Diehl (1979) to represent subtidal and intertidal environments.

The transition sediments, therefore, represent a reduction in storm energy and an overall shoaling of grand cycle A. The change in depositional conditions is inferred to reflect the establishment of a carbonate

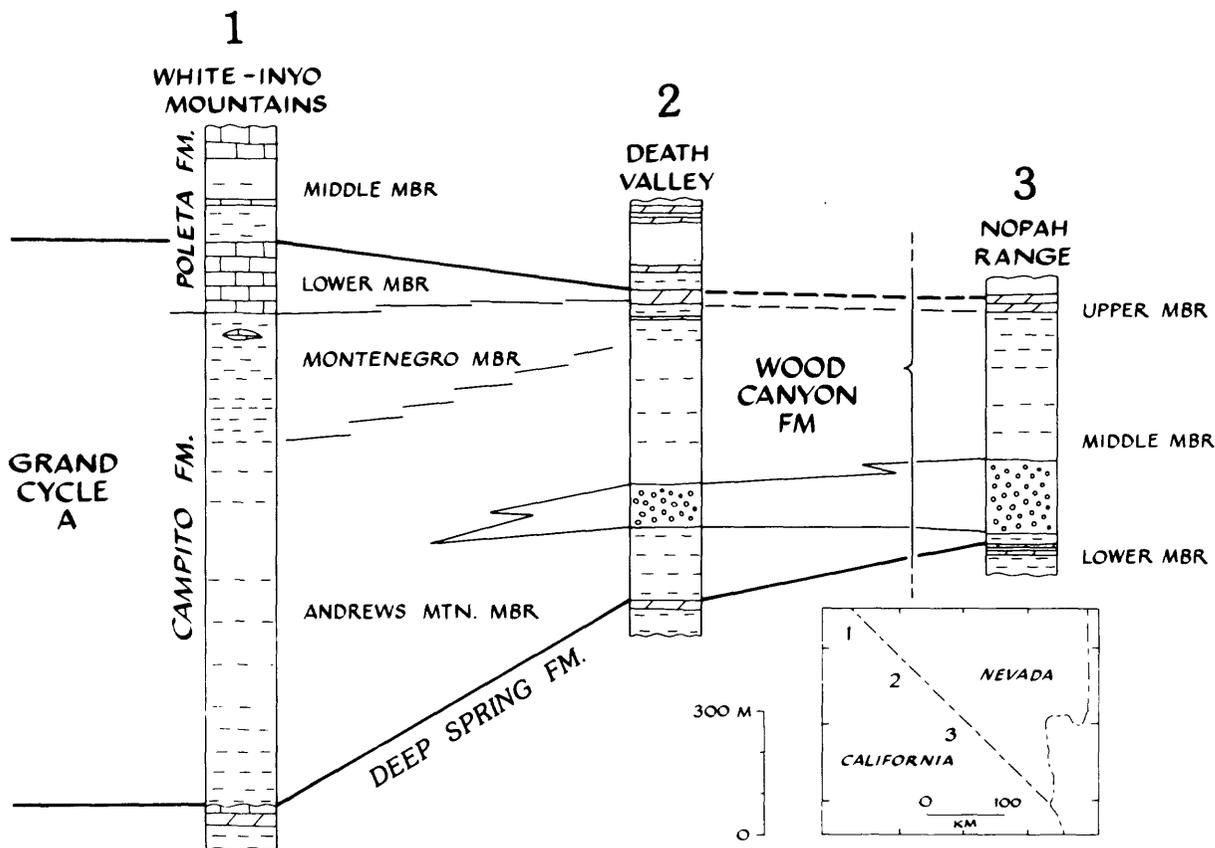


Figure 1.--Regional stratigraphy of Grand Cycle A units in the southern Great Basin, western United States.

barrier seaward of the White-Inyo Mountains area (fig. 2B). This barrier presumably intercepted much of the storm energy that had previously controlled sedimentation, leading to the development of back-shoal lagoon and peritidal conditions. Rowland (1978) has shown that the contact between the terrigenous clastic sediments of the Campito and the overlying Poleta Formation is irregular and diachronous. For example, in some localities, such as the Weepah Hills of Esmeralda County, Nev., thick carbonates were contemporaneously deposited with the more typical Montenegro siliciclastic units. This suggests that the hypothesized shoal was a time-transgressive equivalent of the carbonates of the lower member of the Poleta Formation.

#### Carbonate Half-Cycle

The carbonate half-cycle of grand cycle A is represented in the White-Inyo Mountains by the lower member of the Poleta Formation and in the Death Valley area by the correlative limestone beds within the upper member of the Wood Canyon Formation.

Depositional environments in these sediments have been interpreted by Moore (1976) and Rowland (1978). As suggested by Rowland (1978), these carbonates ultimately developed into a 50-km-wide mosaic of archeocyathid-algal reefs, oolite shoals, islands, and lagoons that interfingered landward with peritidal siliciclastic sediments of the upper member of the Wood Canyon Formation. Beginning with an inferred migrating carbonate shelf, this final grand cycle episode reflects a time when sediment production was eventually able to keep pace with sea-level rise.

#### PROPOSED MECHANISM

As we first suggested in 1979 (Mount and Rowland, 1979), the succession of facies seen in grand cycle A in the southern Great Basin is most easily explained by changes in the rate of relative sea-level rise. The Early Cambrian was a time of major world-wide transgression (Matthews and Cowie, 1979), so there is little doubt of a eustatic sea-level rise during this epoch. Nor is there any question that the Cordilleran miogeocline was subsiding. We imagine

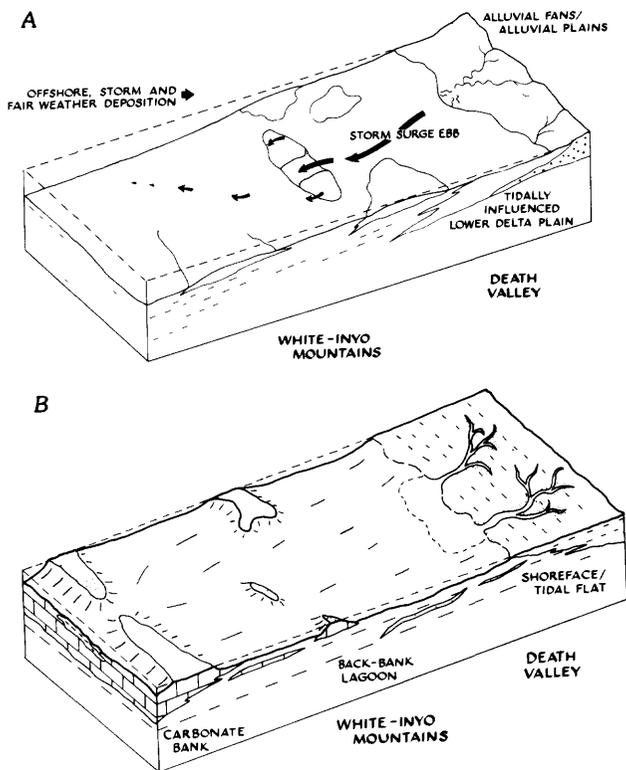


Figure 2.--Depositional systems of Grand Cycle A. **A**, terrigenous clastic half-cycle; **B**, transitional strata and time-transgressive carbonate half-cycle.

both eustatic sea-level rise and basin subsidence to have played key roles in the development of grand cycle A.

The changes in the rate of relative sea-level rise are represented by the change in slope of the schematic curve shown in figure 3. The initial phase, emergence, is represented by the carbonate sediments (top of the Deep Spring Formation) that immediately underlie grand cycle A. These formed a peritidal carbonate bank. If relative sea level falls, as it evidently did here, erosion occurs and a disconformity is left within the record.

The second phase reflects a rapid rise in relative sea level, accompanied by widespread terrigenous clastic deposition (Andrews Mountain Member of the Campito Formation). This is a somewhat anomalous event in that a rapid rise in relative sea level would normally be expected to drown nearby source lands and stop the deposition of coarse clastic sediments. In this case, however, there was a supply of terrigenous clastic material that accumulated in peritidal environments during the initial phase that was ready to be transported into deeper water. Palmer and Halley (1979) have documented the progradation of

terrigenous clastic sediments during periods of relative sea-level stasis in the Lower and Middle Cambrian Carrara Formation of the southern Great Basin. Such sediments, we propose, are temporarily ponded in paralic and coastal reservoirs where there is insufficient energy available to move them across the shelf into deeper water. With a rapid rise in relative sea level, wave energy becomes available to transport the sediment seaward (a concept originally suggested by R. A. Price in Aitken, 1966).

The mixed clastic and carbonate deposition (Montenegro Member of the Campito Formation) represents the third phase of grand cycle A. These transitional strata between the two half-cycles reflect a reduction in the rate of relative sea-level rise. The inferred slowdown in the rate allowed shoaling of the shelf to begin. A carbonate shoal began to develop on the outer shelf, reducing the energy on the inner shelf.

In the last phase of grand cycle A, carbonate production kept pace with sea-level rise, expanding into a broad carbonate reef-oolite shoal-lagoon complex (lower member of the Poleta Formation). At this point the rate of relative rise was very slow. Although the carbonate facies expanded landward during this phase, terrigenous sediment doubtless continued to be supplied from the emergent craton. As discussed earlier, this material was probably ponded in peritidal and alluvial environments on the inner shelf. If eustatic sea level were to completely stop, a prograding clastic facies would ultimately override and terminate carbonate production. Palmer and Halley (1979) have shown this to be the normal progression in the Carrara Formation, although it does not always reach the point of completely shutting off carbonate production.

The cycle was now complete. A new pulse of rapid relative sea-level rise initiated the next grand cycle.

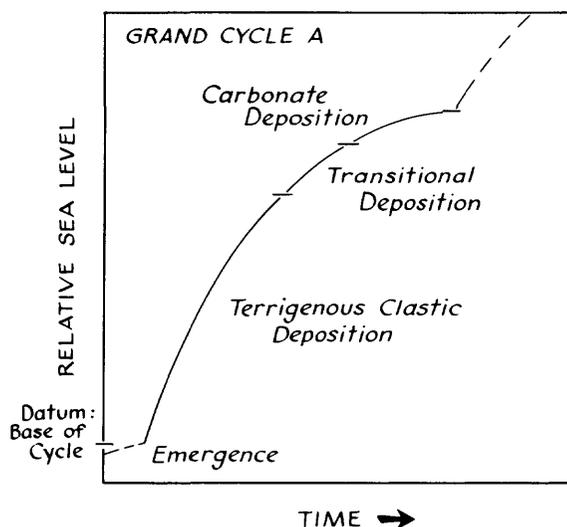


Figure 3.--Schematic relative sea-level curve for Grand Cycle A.

## SUMMARY AND CONCLUSIONS

In his reexamination of the original grand cycle concept, Aitken (1978) pointed out that no two grand cycles are alike, and each one may reflect unique depositional circumstances. This is certainly true of grand cycle A in the southern Great Basin. In contrast to other grand cycles, it is markedly thicker and more siliciclastic-rich, and contains a distinctive, framework-building fauna. However, three fundamental depositional events are recorded in all grand cycle studies. These are: (1) A deepening is associated with the initiation of widespread terrigenous clastic deposition, (2) The transition between the terrigenous clastic half-cycle and the overlying carbonate half-cycle is diachronous and irregular, (3) Widespread carbonate deposition toward the latter part of the cycle is associated with laterally prograding peritidal banks. As shown in the previous discussion, the succession of depositional environments in grand cycle A is most easily explained by a decrease in the rate of relative sea-level rise. Whether the underlying mechanism for this or any grand cycle is a pulsating eustatic sea level or variations in the rate of subsidence is not yet certain. However, grand cycles turn out to be correlative throughout the cordillera, as Fritz's (1975) work suggests, then some mechanism must be applied that affects the entire region. Rather than invoking complex variations in sediment supply, regional uplifts, or miogeoclinal subsidence within a passive margin setting, cyclic changes in the rate of eustatic sea-level rise would be the most effective, externally-derived mechanism. If grand cycles are controlled by pulsating eustatic changes, then correlative cyclic sequences should be recognized on shelves of other continents as well. A complete analysis of this problem awaits more precise interregional and intercontinental correlations of Cambrian strata.

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#### 44. ARTHROPODS WITH PHOSPHATIZED SOFT PARTS FROM THE UPPER CAMBRIAN "ORSTEN" OF SWEDEN

By

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Etching of black nodular limestones (orsten) from the Upper Cambrian in southern Sweden with 15 percent acetic acid produced an unexpectedly varied arthropod fauna with preserved appendages. The etching was done on a set of plastic screens, to avoid breakage during the washing and rinsing. Although preparation still is in progress, more than a thousand specimens are available now and some of the representatives are described here.

##### OSTRACODES

The ostracodes are by far the most common and widespread fossils preserved in samples studied. Appendages of the phosphatocopid genera Falites and Vestrogothia have been described in detail (Müller, 1979). Abundant material of the genus Hesslandona was found in the Agnostus pisiformis Zone. Hesslandona has a carapace with a ventral bar that is separated from the valves by two nullidont hinge lines. As similar articulation structures have not been observed elsewhere in the Ostracoda, the designation of Hesslandona as a member of the subclass Ostracoda was questioned by Adamczak (1965) and Kozur (1974).

The preserved soft organs now prove with certainty that Hesslandona is an ostracode (fig. 1). The new material clearly illustrates seven appendages. The first antenna of Hesslandona is uniramous, which is in contrast to Falites and Vestrogothia, where it is clearly biramous. Hesslandona has a large tripartite organ at the front of hypostome. Its position in the middle between the first antennae suggest that it is homologous to the median eye of other Ostracoda. The median organ is covered by a thin membrane which on some specimens was blown up like a balloon. This may be no more than a peculiar state of preservation caused by the internal generation of gas due to decomposition of tissue at the time of burial.

The second and third appendages are similar to one another, being large and biramous. The exopodites are composed of 20-23 podomeres, each of them bearing a long seta. The endopodites have elongated endites, which presumably served for feeding. No specialized mandibulae and maxillae are developed.

Appendages four to six have exopodites differentiated as respiration organs with well developed vibratory plates, and endopodites with protruding endites for feeding (fig. 2).

Hesslandonids are more similar to the extant orders of Ostracoda than Falites and Vestrogothia.

##### CEPHALOCARIDA

The Cephalocarida Sanders (1955) were recorded hitherto from the Holocene only. The Late Cambrian Dala peilertae (fig. 3) is similar in many respects to the extant Hutchinsonella. At present more than 45 specimens of Dala have been collected, and by overlap of detailed morphologic features an almost complete reconstruction has been developed. Two or possibly three different growth stages have been found. The last stage is identifiable as the adult, because three pairs of reproductive bulbs have developed at the posterior end of the body; the other, somewhat smaller stages, do not have these. No stages younger than these two or three have been found.

The frontal region bears two pairs of biramous appendages. The first ones are larger than the thoracopods, but their distal portions are not preserved. Eight limbs have been developed. Most of them are well represented in the collection and have been studied in some detail (fig. 4). They are similar to one another, and differences occur mainly in the coxopodites. The precoxa is composed of eight short annulae, which are similar to each other. The pre-epipodites are semicircular and appear somewhat inflated. The pre-epipodites probably served for mastication and transport of food to the mouth.

The coxopodites bear endites. Their setae, together with the setae on the pre-epipodites, form continuous rows. The number of endites on the coxopodites varies with the position of the limb, and this feature proved useful for the reconstruction. On the second to fifth post-oral appendages are five endites, on the sixth post-oral appendages four endites, and on the seventh appendage only two endites. The number of endites of the first and last limbs is not discernible in my material. The basipodites of all thoracopods uniformly have two endites. The endopodites are composed of four podomeres, the last

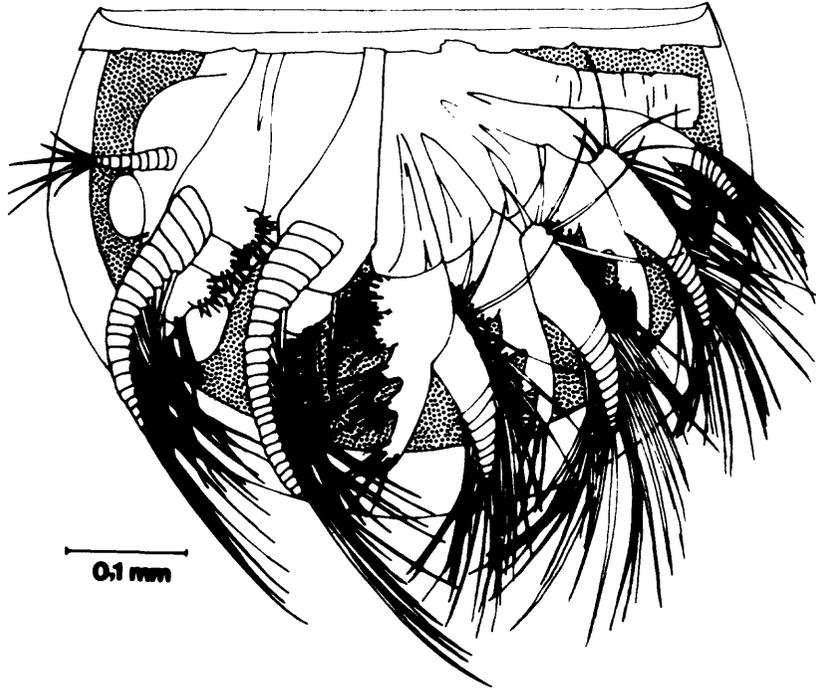


Figure 1.--Reconstruction of the ostracode Hesslandona.

one being distinctly paddle-shaped. The exopodite is composed of an elongated proximal podomere and a paddle-shaped distal one. The latter developed sensory bristles on its outer side (fig. 4). Two distinct lines on the ventral side of the body are considered homologous to the feeding groove of some extant cephalocarids.

The abdomen is composed of four segments, which postero-ventrally bear two characteristic parallel rows of small bristles. It is followed by a telson with furca. The reconstruction shown in figure 4 may require minor modification if more material becomes available.

Because of its restricted biotope, the Cephalocarida had escaped recognition for a long time. It is remarkable that the Late Cambrian representative has been found in an environment of very soft sediment, similar to the modern environment of this, little change seems to have occurred in the living conditions of the group for 500 m.y.

#### LARVAL FORMS FOR ARTHROPODS

As could be expected in an association of soft-bodied animals in a size range below 1 mm, larval stages of various groups have been encountered. The source rock is a trilobite breccia. Although the fossils of this formation have been studied in detail for more than 150 years, no larger crustaceans hitherto have been recorded. The phosphatization obviously is

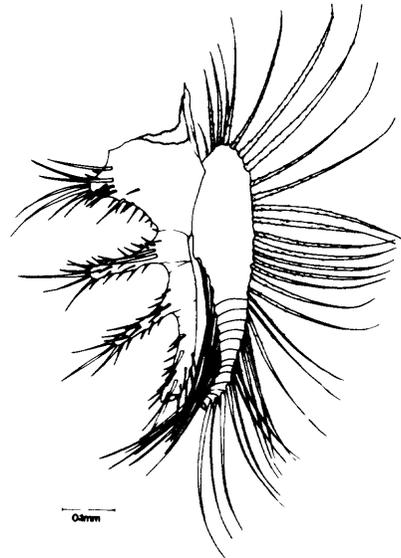


Figure 2.--Large fifth appendage of Hesslandona, found disjunct (setae slightly restored).

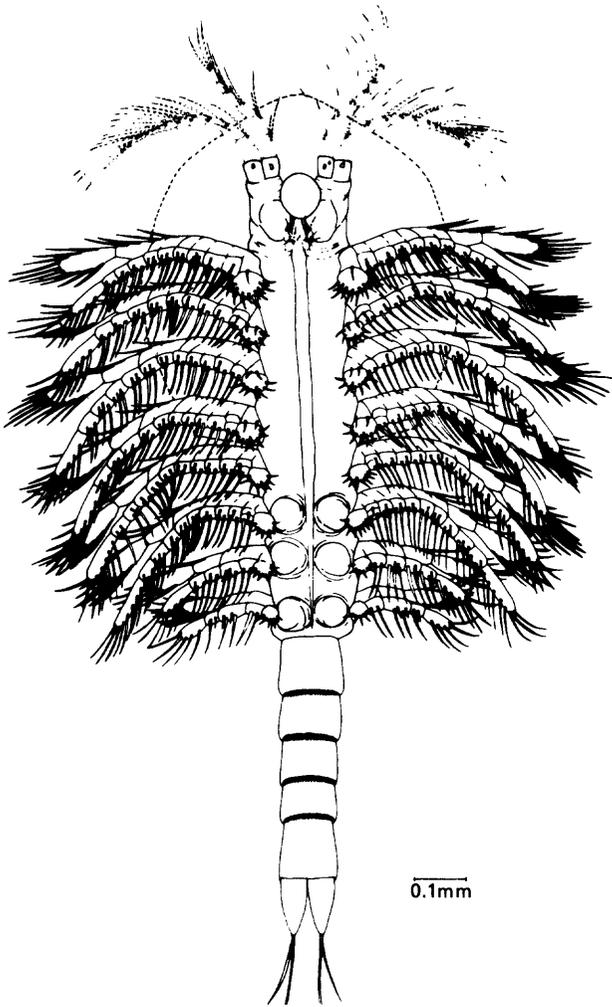


Figure 3.--Reconstruction of the cephalocarid Dala peilertae.

restricted to small objects, and the adults belonging to these larvae are unknown. As an example, a metanauplius stage of a crustacean is presented (fig. 5). Its most obvious feature is the large hypostome. The anterior structure is tentatively regarded as being equivalent to the lateral eyes. It is composed of two bulbous extensions connected in the middle by a bridge, which has a small depression at its center, possibly corresponding to the median eye. There are one pair of uniramous appendages, two pairs of biramous appendages bearing long setae, and a partially developed pair of limbs. The abdomen exposes telson and furca. The carapace is univalved. Other metanauplius stages, belonging to different crustacean groups, have as many as five such pairs of partially developed limbs.

Another interesting form has a univalved cephalothorax and a well developed abdomen, which is composed of 11 segments plus telson with furca (fig. 6). The seventh through ninth segments each bear three characteristic sharp ventral spines. No subdivision into tergites and sternites can be recognized on the pleomeres. The short body has 5 or 6 pairs of appendages, all being long and biramous (fig. 7), except for the first pair.

Very small larval stages (fig. 8) have three pairs of appendages, which seem to correspond to three pairs of short, node-like extensions on the ventral side. The relation between these elements is not clear. Only the second pair branches in its distal part; the others are uniramous. On the dorsal side a single, large, coniform protrusion is present, and at the posterior end a small abdomen with a short telson is developed. A mouth or anus has not been observed. A detailed analysis has not yet been completed, and it is hoped that larger growth stages will be discovered in future preparations.

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(Figures follow)

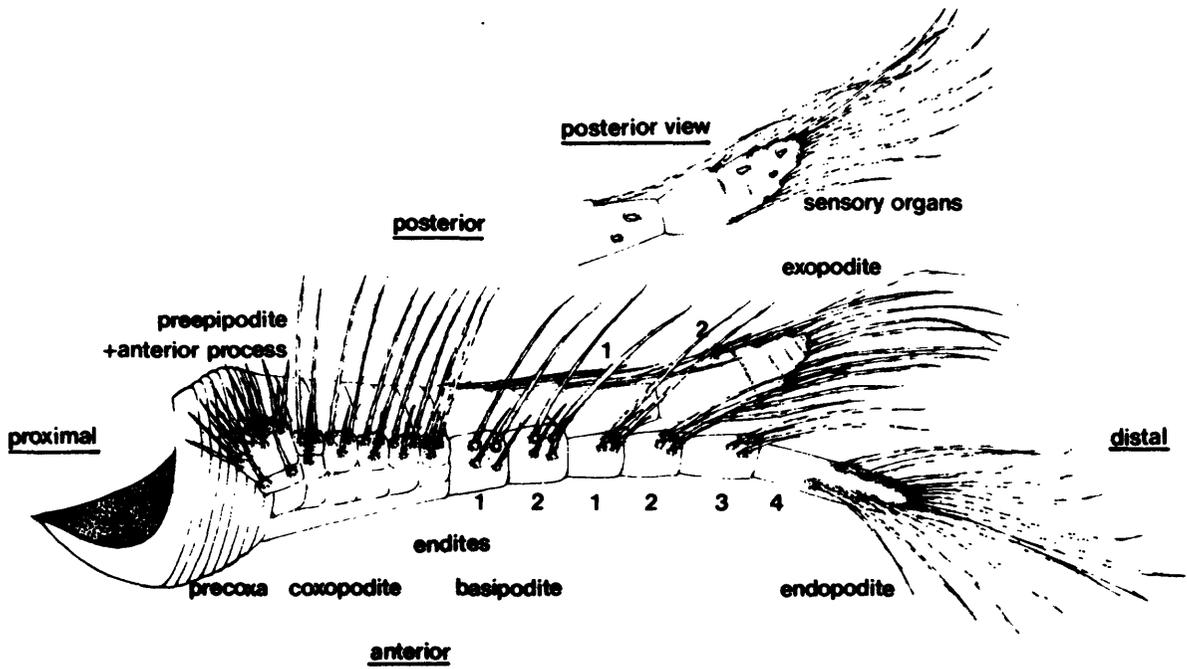


Figure 4.--Reconstruction of the appendage of Dala.

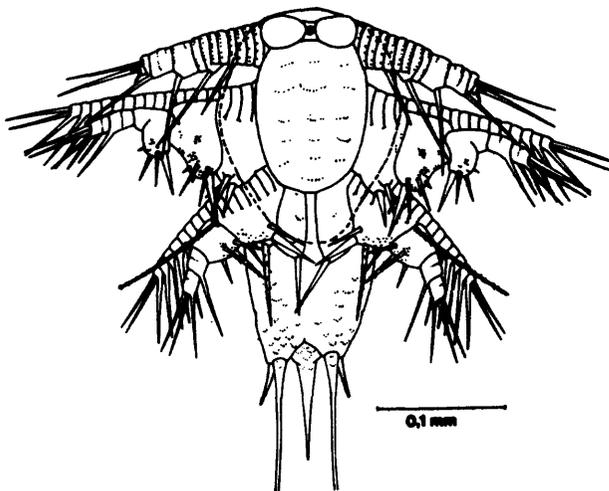


Figure 5.--The meta-nauplius larva of a crustacean.

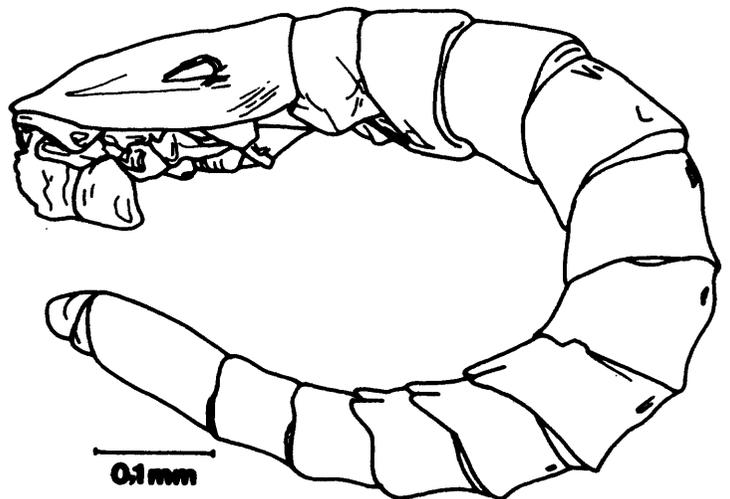


Figure 6.--Complete specimen of an undescribed crustacean.

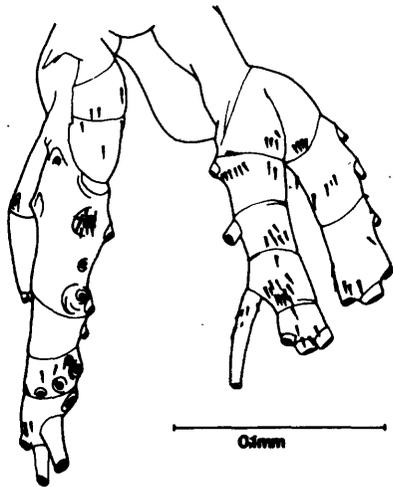


Figure 7.--Biramous posterior appendages of another specimen of the same species as shown in figure 6.

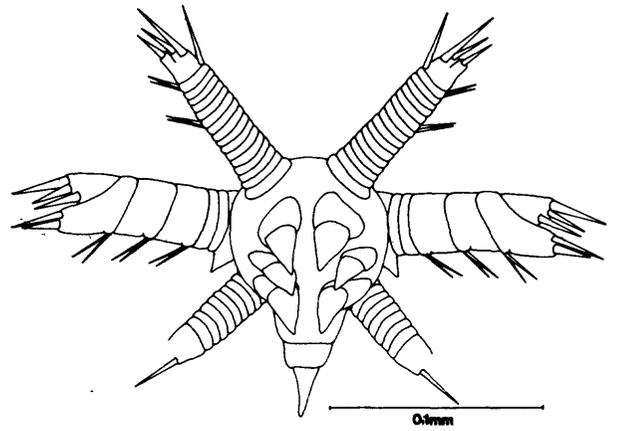


Figure 8.--A parasitic(?) larval stage of an unassigned arthropod.

## 45. REVIEW OF POTENTIAL STRATOTYPE SECTIONS FOR THE CAMBRIAN-ORDOVICIAN BOUNDARY IN CANADA

By

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A summary of the present status of knowledge of the Cambrian-Ordovician boundary interval in Canada naturally presents a survey of the recent work of many scientists, including Barnes, Dean, Erdtmann, F  hraeus, Jackson, Kindle, Landing, Ludvigsen, Nowland, Skevington, Taylor, Tipnis, and Whittington.

In Late Cambrian and Early Ordovician time, Canada was part of the stable, partly emergent North American craton bordered by carbonate platforms and, beyond these, by deeper marine environments (Text-fig. 1). The carbonate platforms were broad in the west with complex facies belts; in the east they were narrower. The outboard margins of the platforms are preserved locally in western Newfoundland, in northeastern British Columbia, and in the northern Yukon, and show complex suites of rocks that include breccia beds with transported biogenic assemblages derived from adjacent platforms, interbedded with fine-grained sediments that have deeper water and pelagic assemblages. Turbidites are present in some of these marginal environments, and also are known within the central regions of the Richardson Trough of the northern Yukon and of the Hazen Trough of northern Ellesmere Island.

Currently many studies are concentrating on the boundary interval. Most of these have focused on the Trempealeauan-Canadian boundary (and its lateral equivalents in deeper marine facies) as the preferred level, but many have extended higher to include coverage of the Tremadocian-Arenigian level and its equivalents. The groups of fossils under intensive study are conodonts, trilobites, and graptolites; some attention also is being given to brachiopods and acritarchs.

In southwestern Alberta, biostratigraphic studies of rocks within the carbonate platform have yielded details of the sequences of conodont and trilobite zones at Mount Wilson and at Wilcox Pass (Aitken and Norford, 1967; Derby and others 1972; Dean, 1977, 1978; Kennedy and Barnes, 1981) that are remarkably similar to those in Oklahoma, Nevada, and Utah--particularly so near the base of the Missisquoia Zone. At Mount Wilson, this horizon is about 20 m above the base of the Survey Peak Formation, and about 2 m above the base of the Cordylodus proavus Zone. The top of the Tremadocian probably correlates within trilobite Zone G of Ross (1949). The base of zone G at

Mount Wilson is about 350 m above the base of the Missisquoia Zone, and the trilobite and conodont faunas of the total interval now are relatively well established. The southwestern Alberta sections are situated too far inside the outboard edge of the carbonate platform for the occurrence of any but the rarest graptolites, and correlation with the standard sequences of graptolites is tenuous.

In the Ware Map-area of northeastern British Columbia, the Kechika Formation can be interpreted as having been deposited near the outer margin of the carbonate platform (Cecile and Norford, 1979). The Kechika becomes more argillaceous westward, and the upper part changes facies into the overlying Road River Group that represents deeper deposition. Trilobites and rare graptolites are present in the Kechika, but as yet are unstudied. The conodont faunas are known (Tipnis, 1981 and unpub. data) and show mixing of North Atlantic and Midcontinent assemblages. Kechika informal units OK2, OK3 and lower OK4 can be correlated with the Tremadocian. The interval OK2 to lower OK4 is about 900 m thick at the Grey Peak Section, with the first appearance of Cordylodus proavus at 3.5 m above the base of unit OK2 and about 70 m above the base of the Kechika.

Farther north, the Nahanni Map-area of westernmost District of Mackenzie shows both the carbonate platform and the coeval shale basin. Studies by Landing and others (1980), and by Tipnis and others (1979) of stratigraphic sections near the outer edge of the platform reveal that the uppermost part (about 100 m) of the Rabbitkettle Formation can be correlated with the Tremadocian by means of its conodont and trilobite faunas. The basal part of the overlying Road River Group is poorly fossiliferous but higher beds contain lower Arenigian conodonts. Graptolites seem to be lacking from the succession but R. Ludvigsen (unpub. data) has established a detailed comparison of the sequence of trilobite faunas with those of the interval Saukia Zone to Symphysurina Zone in Alberta and in the western United States.

In the Richardson Trough of the northern Yukon Territory, the upper member of the Road River Group contains graptolitic shales and turbidites and boulder beds derived from the adjacent carbonate platforms. As yet no program has been carried out to sample the beds of allochthonous carbonate. Jackson (1974, 1975)

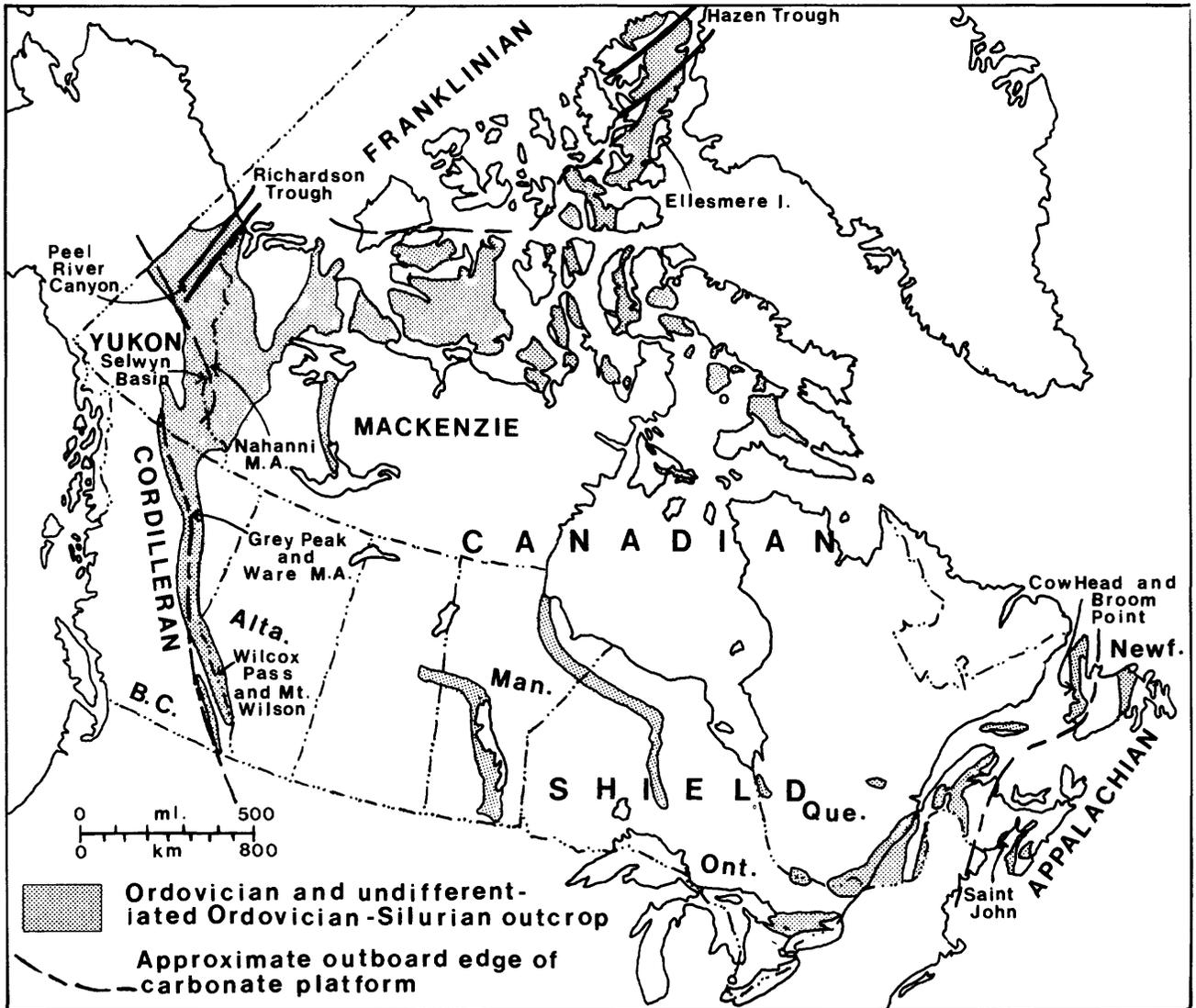


Figure 1.--Distribution of main Ordovician outcrops and undifferentiated Ordovician-Silurian outcrops in Canada. The Cordilleran, Franklinian, and Appalachian orogens are marginal to the Canadian Shield that formed the stable craton during the Ordovician.

has established a sequence of Tremadocian graptolite zones as *Staurograptus tenuis*, *Anisograptus richardsoni*, *Clonograptus aureus* and *Adelograptus antiquus* in about 136 m of strata in the Peel River Canyon, and unpublished identifications by Norford substantiate this sequence farther south in the Selwyn Basin. The Road River Group extends many hundreds of meters below Jackson's Peel River interval, and although Upper Cambrian trilobites and dendroid graptolites have been collected from some horizons, no rigorous attempt has been made to collect the faunas below the *Staurograptus tenuis* Zone. Similarly, the conodont faunas of the whole sequence are not yet known.

In eastern Canada, at Saint John, New Brunswick, discontinuous outcrops of dark shales with limestone concretions seem to represent fairly deep-water deposition, and provide data important to correlations of lower Tremadocian strata of eastern North America with the succession of the Oslo Region (Landing, 1980; Landing and others, 1978). Taxa vital to intercontinental correlations are present (including *Cordylodus proavus*, *Dictyonema flabelliforme parabola* and *D. flabelliforme sociale*), but the succession is incompletely exposed and the upper Tremadocian and basal Arenigian parts are poorly known.

The Cow Head Group of western Newfoundland is well exposed in extensive shore outcrops. It consists of shales and platy limestones with interbedded limestone breccias derived from a carbonate platform that was to the north and northwest. Sequences of faunas are known both from the shales and platy limestones (graptolites and trilobites) and from blocks within the breccias (trilobites, conodonts). At Cow Head, a complex sequence seems to span the entire Tremadocian in about 60 m of strata between beds with Upper Cambrian blocks (bed 6) and shales (termed 8f) that contain graptolites indicating the Tetragraptus approximatus Zone (Kindle and Whittington, 1958, p. 319-325; Fähræus and Nowlan, 1978; James and others, 1980, p. 23-30). Recent studies at Broom Point (Fortey and Skevington, 1980) have demonstrated limestone breccias bearing trilobites of the Missisquoia Zone about 5 m below other breccias with trilobites of the Symphysurina Zone. The intervening shales contain four graptolite bands, in ascending order characterized by Radiograptus rosieranus, Dictyonema flabelliforme of the parabola type, D. flabelliforme sociale, and Staurograptus sp. together with a different subspecies of D. flabelliforme. The stratigraphic thicknesses are small and the biostratigraphic significance of these faunules needs to be fully demonstrated, particularly whether the Radiograptus band lies within the range zone of Dictyonema flabelliforme or entirely lower.

#### CONCLUSIONS

Each of the localities discussed contributes to our knowledge of the Tremadocian interval in Canada, and detailed studies are continuing on most of the stratigraphic section. The exposures are excellent at each locality except Saint John. Conodonts and trilobites are known from all localities except the Peel River Canyon, but graptolites essentially are absent or are rare in the sections in southwestern Alberta, northeastern British Columbia, and westernmost Mackenzie. The sections at Broom Point and Cow Head in western Newfoundland have excellent potential for the integration of zonal schemes based on graptolites, trilobites, and conodonts.

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## 46. ON THE CORRELABILITY OF GRAND CYCLE TOPS

By

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Cambrian Grand Cycles (Aitken, 1966) consist of a lower unit of predominantly clastic rocks and an upper unit of predominantly carbonate rocks. Thicknesses range from a few tens of meters to several hundred meters. The upward transition from clastics to carbonates is characteristically gradual, and the upward transition from the carbonates of one Grand Cycle to the clastics at the base of the next is almost always abrupt.

Both Aitken (1978) and Palmer and Halley (1979) have interpreted the mechanism of formation of Grand Cycles to be a reflection of differential rates of basin subsidence and (or) sea-level rise. Discrimination between these two possibilities rests on the regional correlatability of the sharply defined Grand Cycle tops.

To test this, Cambrian sections throughout North America were examined for abrupt upward changes from carbonates to clastics and the ages of these changes, determined with trilobite control, were located on a correlation chart as accurately as possible. A selection of sections showing the distribution of possible Grand Cycle tops is shown on figure 1. At least four or five of these tops can be recognized from northern Mexico to the southern Canadian Rockies, a distance of about 2500 km. The three oldest tops, all in the Lower Cambrian, seem to be recognizable for an additional 1200 km northward into the Mackenzie Mountains, (fig. 1, col. Q). This would seem to be a strong point for a primary eustatic control on the driving mechanism of Grand Cycles. However, there are few demonstrable Grand Cycle tops in Cambrian sections from Alaska across the Arctic Region, and southward throughout the Appalachian region, with one exception. In eastern Tennessee, three possible Grand Cycles can be identified. One, composed of the Rome and Rutledge Formations terminates at about the top of the *Glossopleura* zone (fig. 1 col. X) approximately equivalent to the top of cycle 6 in the southern Cordilleran region. The two other possible cycle tops, between the archaeocyathid-bearing Shady Formation and the Rome Formation in the Lower Cambrian, and between the Maryville Limestone and Nolichucky Shale in the Upper Cambrian, have no Cordilleran counterparts (fig. 1, cols. W and Y), however.

Although cycle tops 1-4, 6, and 8-10 in the southern Great Basin seem to have equivalents in the southern Canadian Cordillera, some distinctive cycle tops are found only in the Great Basin region, raising further questions about eustatic control.

Additional complications in interpreting the tectonic significance of cycle tops may be caused by the fact that some cycle tops are overlain by outer detrital belt sediments and others by inner detrital belt sediments.

In cycle top 3, when the beds above the cycle top represent the outer detrital belt, they seem to be of early Middle Cambrian age, whereas, when the overlying beds represent the inner detrital belt, there are olenellids present for the first few meters of the new Grand Cycle and the top is clearly within the Lower Cambrian. The physical correlations of this cycle top are strong, so either the top is slightly diachronous, or there is an as yet unresolved biofacies problem.

In cycle top 8, the part overlain by outer detrital belt sediments is believed to be slightly older than that overlain by inner detrital belt sediments (Robison, 1976). Again, the age discrepancy is small, and it may be an artifact of the difficulty of precisely correlating trilobites of different biofacies.

In cycle top 10, at the base of the widespread Dunderberg Shale, the age of the change to outer detrital belt sediments varies by one or two trilobite zones even within the Great Basin. Despite this variation, the age appears to be approximately that of the top of the Sullivan-Lyell Grand Cycle, which is one of the two "classical" Grand Cycles of Aitken. However, the top of that cycle may be a reflection of the regional disconformity between the Dresbachian and Franconian Stages.

The Lyell limestone in Canada has produced only trilobites of *Aphelaspis* Zone or older age. In the lowest meter or two of the overlying Bison Creek Formation, I have collected *Elvinia* and only a few meters higher, *Irvingella*. Thus, here the beds just above the cycle top are indicative of the *Elvinia* Zone, several trilobite zones younger than the beds adjacent to cycle top 10 to the south; the apparent correlation of this cycle top and its equivalents, that are overlain by inner detrital belt clastics, with the cycle top below the Dunderberg Shale may be spurious.

Despite the problems, the fact that so many of the Grand Cycle tops can be correlated from the southern Great Basin to at least the southern Canadian Cordillera, and that the three oldest tops perhaps can be correlated from Mexico to the northern Canadian Cordillera, suggests some commonality to the sedimentary history of this region. But only the Great Basin seems to have a really continuous record of Cambrian sedimentation. Perhaps the Great Basin region was in the central part of a great subsiding shelf basin; subsidence of this basin during a time of general global sea-level rise was episodic and, in its central part, exceeded the rate of eustatic lowering of sea level that is reflected across the remainder of the continent in late Early Cambrian and again in late Dresbachian time. The correlatability of Grand Cycle tops seems to be widespread within the present southwestern quadrant of the continent. However, absence of evidence for clear correlatability in the remainder of the continent suggests that primary eustatic control as a causative factor is not the answer.

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(Figure 1 follows)



Cycle top 6: Top of limestone unit terminating at or slightly below top of Glossopleura Zone. Column C, lower unit of Papoose Lake Member, Bonanza King Formation, Nevada and California; Column D, Burrows Limestone, Pioche region, Nevada; Column I, middle Ophir Formation limestone, Tintic District, Utah; column J, upper Langston Limestone, Bear River Range, Utah; column K, High Creek Limestone, southeastern Idaho; column N, Damnation Limestone, Montant Thrust Belt; column O, Cathedral Formation, southern British Columbia; column P, Mumm Limestone, Mt. Robson, British Columbia; Column R, Rutledge Limestone, eastern Tennessee. (Palmer, 1971a,b; Oriol and Armstrong, 1971; Lochman-Balk, 1971; Aitken, 1978, Walcott, 1913).

Cycle top 7: Top of limestone terminating within the Ehmaniella Zone. Column H, Dome Limestone, House Range, Utah (Robison, 1976).

Cycle top 8: Top of limestone terminating in or slightly above Ptychagnostus gibbus Zone. Column C, Papoose Lake Member, Bonanza King Formation, Nevada and California; column D, Step Ridge Member, Highland Peak Limestone, Pioche region, Nevada; columns E and F, Geddes Limestone, Eureka district and northern Egan Range, Nevada; column G, Pole Canyon Limestone, Snake Range, Nevada; column H, Swasey Limestone, House Range, Utah; columns J and K, Blacksmith Formation, northern Utah and southeastern Idaho; column N, Dearborn Limestone, Montana Thrust Belt; Column O, Eldon Formation, southern British Columbia (Palmer, 1971a; Robison, 1976; Lochman-Balk, 1971; Aitken, 1978).

Cycle top 8a: Top of limestone in middle part of Bolaspidea Zone. Columns O and P, Arctomys Formation, Mt. Robson and southern part of British Columbia (Walcott, 1913, Aitken, 1978).

Cycle top 9: Top of limestone very close to the top of the Bolaspidea Zone. Column D, member J, Highland Peak Formation, Pioche region, Nevada; column G, limestone member in middle of Lincoln Peak Formation, Snake Range, Nevada; column H, Marjum Formation, House Range, Utah; columns J and K, middle limestone member, Bloomington Formation, northern Utah and southeastern Idaho; column L, Death Canyon Member, Gros Ventre Formation, northwestern Wyoming; column M, Meagher Formation, central Montana; column N, Steamboat Limestone, Montana Thrust Belt; column O, Waterfowl Formation, southern British Columbia (Palmer, 1971a, Lochman-Balk, 1971, Aitken, 1978).

Cycle top 10: Top of limestones terminating within the Aphelaspis Zone. Column C, Banded Mountain Member, Bonanza King Formation, Nevada and California; column D, lower member, Mendha Limestone, Pioche region, Nevada; column E, Hamburg Formation, Eureka District, Nevada; column F, Raiff Limestone, northern Egan Range, Nevada; column H, Big Horse Limestone Member, Orr Formation, House Range, Utah; (Palmer, 1971a).

Cycle top 11: Top of limestone terminating in or near the base of the Elvinia Zone. Columns G and H, Johns Wash Limestone, Snake Range, Nevada and House Range, Utah (Palmer, 1971a).

Cycle top 12: Top of limestone terminating at the top of the Irvingella major subzone of the Elvinia Zone. Column F, lower limestone member, Windfall Formation, Eureka, Nevada; column G, Barton Canyon Limestone Member, Windfall Formation, northern Egan Range, Nevada (Palmer, 1971a).

## 47. SUBDIVISION OF THE SAUK SEQUENCE

By

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The Sauk sequence is the oldest of a series of system-size, unconformity-bounded Phanerozoic sedimentary sequences in North America proposed by Sloss (1963). It includes rocks ranging from late Precambrian through Early Ordovician in age and is most fully represented in the southern cordilleran region of western North America. It is from this region that the characteristic Cambrian through Lower Ordovician biostratigraphy of North America has been developed (fig. 1). Intercontinental correlation of the North American faunal zones has always been most difficult for the early Middle Cambrian and, more recently, for the interval represented by the Late Cambrian Pterocephaliid Biome. Regional analysis of some discontinuities in North American Cambrian sections may provide an explanation for these correlation difficulties.

When the biostratigraphy of the Late Cambrian Pterocephaliid Biome was worked out (Palmer, 1965), it confirmed suggestions made earlier on the basis of physical stratigraphy that a disconformity separated rocks of Dresbachian Age from younger rocks of Franconian Age over large areas of the western United States. In many areas, beds with faunas of the Elvinia Zone, above the disconformity, are separated by only a few meters from beds with faunas of Prehousia Zone or, more commonly, Aphelaspis Zone age; faunas representing the Dunderbergia and some earlier zones in the middle of the Pterocephaliid Biome are generally missing. Evidence for the disconformity has been recognized in the eastern part of the Great Basin, in the Rocky Mountains from Montana to Arizona, and in the mid-continent region in Texas, Missouri, and the upper Mississippi Valley (Lochman-Balk, 1970). Recently, I made collections that indicate the probable presence of this disconformity in the St. George Limestone on the Port-au-Port peninsula in western Newfoundland, and I have studied collections made by John Peel of the Geological Survey of Greenland, that suggest the presence of this disconformity within the Cass Fjord Formation of northwestern Greenland. Examination of collections made by W. H. Fritz and R. Ludvigsen in the Mackenzie Mountains of northern Canada suggests that the sequence through the Pterocephaliid Biome is incomplete there, as well. Also, in the southern

Canadian Rocky Mountains, the presence of Elvinia at the base of the Bison Creek Formation, which rests on limestones of the Lyell Formation that have only yielded faunas as young as the Aphelaspis Zone, suggests that the disconformity is present there.

The discontinuity in the faunal record seems to be most characteristically developed on the carbonate platform and in the inner shelf regions, and evidence for the Dresbachian-Franconian break now seems to be present across much of the area of late Dresbachian epicontinental sea in North America. In the outer shelf sequence of central British Columbia, Fritz's collections indicate a continuous fossiliferous section through the Pterocephaliid Biome. This is also the primary facies for a continuous record of this interval in the Great Basin.

A less well-established disconformity in the faunal record seems to be present in the highest Lower Cambrian to lowest Middle Cambrian part of the column. North of British Columbia in the cordillera, from Alaska to northeast Greenland, and southward to the southern end of the Appalachians, there is no clear record for most of the early Middle Cambrian trilobite faunas known from the southern cordillera. Characteristically faunas of Glossopleura Zone or younger Middle Cambrian ages are found only a few meters above beds with olenellids. In basinal sequences from northeastern Greenland, western Newfoundland, Vermont, New York, southeastern Pennsylvania, and southwestern Virginia, there is very little stratigraphic interval between beds containing Early Cambrian trilobites and beds containing medial or late Middle Cambrian trilobites. In the miogeoclinal sections of the Appalachian region, the Lower-Middle Cambrian boundary interval is occupied by a major clastic unit, generally sandy or silty, separating marine carbonate sequences. Almost all fossils from this clastic interval are of Early Cambrian age, but very little is known about their precise positions within the interval. In northwestern Newfoundland, collections made by Noel James throughout much of the Hawke Bay Sandstone, which represents this clastic interval here, yield only Early Cambrian fossils. Middle Cambrian faunas from limestones on top of this clastic interval are characteristically Glossopleura Zone age or younger.

Lower Ordovician	N		SAUK III
	M		
	L		
	J		
	I		
	H		
	G <sub>2</sub>		
	G <sub>1</sub>		
	F		
	B		
Upper Cambrian	Saukia	PTYCHASPID BIOMERE	SAUK II
	Saratogia		
	Taenicephalus		
	Elvinia	PTEROCEPHALIID BIOMERE	
Middle Cambrian	Dunderbergia		SAUK II
	Aphelaspis		
	Crepicephalus		
	Cedaria	MARJUMIID BIOMERE	
	Bolaspidella		
	Ehmaniella		
Lower Cambrian	Glossopleura	"CORYNECHOID" BIOMERE	SAUK I
	Albertella-Mexicella		
	"Plagiura-Poliella"		
Lower Cambrian	Bonnia-Olenellus	"OLENELLID" BIOMERE	SAUK I
	Nevadella		
	Fallotaspis		
	"Tommotian"		

Figure 1.--Trilobite biostratigraphy of the Cambrian and Lower Ordovician for North America showing the locations of the proposed subsequence boundaries (Sauk I, II, III) of the Sauk sequence, and their relations to biomere boundaries.

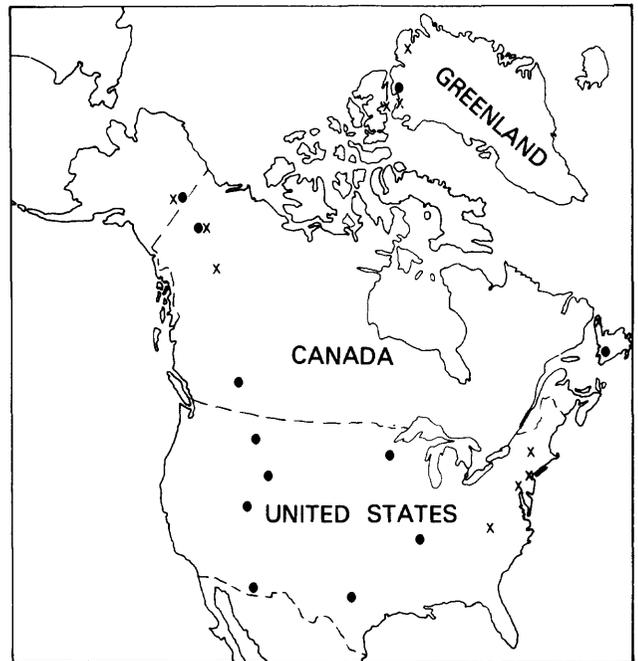


Figure 2.--Map of North America showing localities where the Dresbachian-Franconian (solid circles) and the early Middle Cambrian (X's) discontinuities bounding the Sauk subsequences can be documented.

The widespread record of a faunal discontinuity, or of a clastic unit representing a regional regression towards the end of the Early Cambrian, suggests that this interval also is a reflection of a continent-wide event. No other parts of the North American Cambrian succession have widespread discontinuities comparable to the two that are discussed above. The discontinuity between Lower and Middle Cambrian beds is also widespread in the Baltic region of western Europe and as far south as North Africa (Martinsson, 1974; Fletcher, unpublished correlation chart, 1967). The distribution of these discontinuities suggests that the events which produced them were more likely eustatic than tectonic.

I suggest that, armed with the evidence for two widespread but relatively short-lived eustatic events, near the end of the Early Cambrian and near the end of the Late Cambrian Dresbachian Stage, stratigraphers studying cratonic regimes check their sections again. The physical evidences for these breaks are not obvious, but the possibility that these breaks reflect a eustatic lowering of sea level suggests that they may be represented in many successions on other continents. This possibility has great importance for Cambrian paleogeography and stratigraphy. The Sauk sequence can clearly be divided into three subsequences in North America. If the suggested

eustatic events that mark the boundaries are recognizable in other cratonic sequences, we have a guide to critical levels for placement of revised series boundaries for the Cambrian System. Also, difficulty of correlating to some parts of the well-developed North American Cambrian trilobite biostratigraphy from other parts of the world may be explained if seemingly continuous faunal successions elsewhere actually have unsuspected breaks.

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## 48. PALEONTOLOGY OF CAMBRIAN MOLLUSKS

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In recent years, a widespread renewal of the study of Cambrian mollusks has resulted in much new information from North America, Australia, New Zealand, USSR, People's Republic of China, and Antarctica. We now know that Cambrian mollusks are more diverse than heretofore thought, that many taxa are geographically widespread, that the occurrence of unique structures makes functional analysis a challenging art, and that some Cambrian forms suggest the ways in which various high-level taxa evolved. Much of the new information about Early and Middle Cambrian mollusks is based on small specimens less than 5 mm long and commonly about 1 mm long, and much of the new material is preserved as siliceous or phosphatic replicas of the original shell or shell filling. By Late Cambrian time, many mollusks are of more usual size, and are more readily observed in outcrop. The increase in information about Cambrian mollusks in the past few years suggests that we have just scratched the surface of what can be known, and I believe that the next few years will provide much new and exciting information about the phylum and its early evolution. The rest of this presentation deals with each of the classes of mollusks, and discusses the most recent information about each of them, adding those unpublished data of which I am aware.

### CLASS APLACOPHORA

No undoubted Cambrian aplacophorans are known. Conway Morris (1979a) has tentatively suggested that the Burgess Shale fossil Wiwaxia corrugata (Matthew) might be related to aplacophorans. Wiwaxia has a radula-like structure and is covered with scales (Conway Morris, 1979b). However, one student of the Aplacophora (Amelie Sheltema, written commun., Dec. 1980) noted that inclusion of Wiwaxia would expand the concept of the class Aplacophora beyond acceptable limits. She also noted that "...it certainly does not tax the imagination too much to consider that one of the early, pre-placophorus mollusks could look like that."

### CLASS POLYPLACOPHORA

The occurrence of this class of mollusks in Cambrian rocks has been the subject of much debate. The thoughts of one school have been summarized by Runnegar and others (1979) and Pojeta (1980), who hold that there are at least three genera of Late Cambrian polyplacophorans and that the class may be represented in rocks as old as Early Cambrian. The thoughts of the other school have been summarized by Yochelson (1978, 1979), who does not regard any of the known Cambrian mollusks as belonging to the Polyplacophora.

Polyplacophorans have numerous spicules in the girdle of the mantle surrounding the shell, and some of these spicules have characteristic ridges and shapes (Haas and Kriesten, 1977). In various parts of Eurasia, small blade-shaped fossils called Sachites (Meshkova, 1974) occur in Lower Cambrian rocks. Some of the species of Sachites have shapes and ridges closely similar to the spicules of polyplacophorans. Bengston is presently studying Sachites, and his work will be most welcomed.

J. H. Stitt and J. R. Derby (written commun., August 1978) have found important new material of the mollusk Matthevia from Upper Cambrian rocks of Oklahoma. This material is silicified and contains large specimens that have one deep hole and small specimens that have two shallow holes. In my opinion, this new material reinforces the interpretation that Matthevia is a polyplacophoran.

The specimens having the single deep hole are placed in M. walcotti. They are markedly concave on the posterodorsal side; this concavity fits very well on the convex anterodorsal side of another plate, the two plates forming an angle of about 60° with the horizontal.

The small specimens are of two types. Type 1 is elongated anteriorly-posteriorly, open only on one side, with a subcentral apex on the dorsum, and a deep ventral concavity, at the apex of which are two large shallow holes. Such a shape can readily be interpreted as the terminal valve of a chiton shell. Type 2 is almost equidimensional in length and width, is open at

the anterior and posterior ends, and has a subcentral apex on the dorsum; in ventral view, type 2 valves form a wide-open "V", at the bottom of which are two large shallow holes. These square valves can readily be interpreted as intermediate valves of a chiton.

#### CLASS MONOPLACOPHORA

In the case of the Polyplacophora, the inclusion of the information from the Cambrian record of mollusks does not dramatically change the concept of the class. Polyplacophorans are still multiplated mollusks having a spiculate girdle; only their stratigraphic range is extended. In the case of the Monoplacophora, inclusion of numerous new Cambrian forms in this class dramatically changes its concept.

Knight and Yochelson (1960) in the Treatise listed 25 genera of monoplacophorans. Runnegar and Jell (1976) included at least 123 genera in their concept of the class; their work has been criticized by Berg-Madsen and Peel (1978) and Yochelson (1978, 1979). The superfamily Helcionellacea is an example of how recent work on non-helicely coiled Cambrian univalves lacking a siphuncle has dramatically changed the variety of shell forms included in the Monoplacophora. In the Treatise, the Helcionellacea is classified in the Archaeogastropoda, and it contains only four genera, all of which are Cambrian in age. In 1960, one could almost fully understand the concept Helcionellacea by only knowing the type genus of the type family. In 1976, Runnegar and Jell placed 48 genera in the superfamily, included the superfamily in the Monoplacophora, and gave the Helcionellacea a stratigraphic range of Tommotian-Middle Devonian. On the other hand, Yochelson (1978, p. 183) suggested that the Helcionellacea might be a separate class-level taxon of the Mollusca and limited it to the Cambrian.

I accept the classification of Runnegar and Jell (1976) which leads to the conclusion that Cambrian helcionellaceans show a wide variety of shell form and include such diverse genera as Helcionella, Latouchella, Yochelcionella, Stenotheca, Mellopegma, Scenella, Hypseloconus, Knighthoconus, and a new form from New Zealand, which is laterally compressed and has a pegma-like structure. Specimens of this new form were kindly provided by D. I. MacKinnon.

#### CLASS GASTROPODA

The hallmark of the gastropod shell is three-dimensional or helical coiling. This type of coiling produces an asymmetry of the shell, and often there is an emargination of the aperture such as a sinus or a slit. Asymmetrical coiling is not widespread in any other higher taxon of noncolonial animals, but it does occur in some protozoans and a few cephalopods, cemented pelecypods, worms, and insect larvae. It is

also an ecologically induced variation in a few solitary corals. Several Late Cambrian helicely coiled shells are regarded as gastropods. However, the taxonomic position of asymmetrically coiled Early and Middle Cambrian shells is debated. In particular, the debate centers around the genera Aldanella and Pelagiella; several other names are also available for shells of these general shapes.

Aldanella is as much as 2 mm in diameter, is ordinarily preserved as internal molds, and occurs in Lower Cambrian rocks in North America, USSR, and Australia. Some variation is seen in the shape of the conch and protoconch, but this variation does not even begin to approach the range of variation suggested by Bockelie and Yochelson (1979) for a supposed species of worm from the Ordovician of Spitzbergen, with which they compared Aldanella. The protoconch of Aldanella is well within the range of variation shown by various gastropods, and commonly gastropods show a change in shape or ornament between the protoconch and conch, as do some specimens of Aldanella.

One specimen of Pelagiella is known in which the muscle scars are preserved; reconstruction of the soft parts of this specimen suggests an animal in which the shell was at an angle to the head-foot mass and thus was torted (Pojeta, 1980).

All the argument about Aldanella and Pelagiella may be made moot by a specimen of an asymmetric univalve from the Lower Cambrian of South Australia. This specimen, discovered by Bruce Runnegar (oral commun., Nov. 1980), has a significant spire and an almost opisthobranch-type shell.

#### CLASS CEPHALOPODA

Until recently, Cambrian cephalopods have been placed in only a few genera known from widely scattered places in the world, and they usually have been placed in one family. In 1979, Chen and others named 10 new genera and 26 new species that they considered to be Late Cambrian cephalopods. This diverse Chinese fauna was placed in three orders.

All known Cambrian cephalopods are of Late Cambrian age, and it is generally agreed (Yochelson, and others, 1973; Jell, 1978; Pojeta, 1980), that they probably arose from the helcionellaceans, using the concept of that taxon of Runnegar and Jell (1976). Some helcionellaceans have septa, and some have a prominent tube that might have evolved into a siphuncle. Helcionellaceans of the genus Yochelcionella have a prominent snorkel projecting from the shell. In most species of the genus, the apex of the shell projects over the snorkel; however, in Y. ostentata, the apex of the shell projects away from the snorkel. If the snorkel is regarded as the homologous structure, both exogastric and endogastric forms of Yochelcionella can be defined. In Y. ostentata, the snorkel forms the high point on the shell, and its cavity

is in line with the body of the shell. An organism like Y. ostentata could have been ancestral to the cephalopods in shape, curvature, and the presence of a structure that could evolve into a siphuncle.

#### CLASS ROSTROCONCHIA

This class of mollusks is known throughout the Cambrian. It has a worldwide distribution in Lower Cambrian rocks, Heraultipegma being known from Australia, China, USSR, Europe, and possibly North America. The published Middle Cambrian record is one species from Australia, but an incomplete specimen of Ribeiria is now known from the Middle Cambrian rocks of Maritime Canada. By Late Cambrian time, nine genera of rostroconchs are known; Ribeiria in North America, Australia, and Antarctica; Wanwania in China and Antarctica; Apoptopegma in Antarctica; Pinnocaris, Pleuropegma, Oepikila, Cymatopegma, and Kimopegma in Australia; and Myona in Korea and China.

Rostroconchs are especially important because they likely evolved from the Helcionellacea and gave rise to the Pelecypoda and Scaphopoda. In the Early and Middle Cambrian, various helcionellaceans developed extension of the ventral aperture up the anterior and posterior faces of the shell and at the same time underwent lateral compression of the shell. Forms such as Anabarella and Mellopegma are difficult to distinguish from Heraultipegma in shell form, gapes, and ornament; they are placed in different classes retrospectively and because Heraultipegma has a pegma. However, because they are all so similar in most ways, the conclusion is that rostroconchs arose from compressed helcionellaceans.

#### CLASS PELECYPODA

A major breakthrough in Cambrian molluscan studies in the past 8 years has been the finding of Cambrian pelecypods in North America, Europe, USSR, Australia, and New Zealand. Three or four genera of this class are now known in the Cambrian. Fordilla and Pojetaia from the Lower Cambrian have been named, and the presence of a ligament, muscle scars, and teeth in these genera have been demonstrated. A specimen from the Upper Cambrian rocks of Maryland (Pojeta, 1980) preserves only shape and has not been named. A new genus and species has been described (MacKinnon, in press) from New Zealand, and I thank D. I. MacKinnon for the specimens shown here. The New Zealand species has taxodont dentition, foliated shell structure, and a ligament can be demonstrated.

Yochelson (1981), in a discussion of Cambrian pelecypods, attempted to show that Fordilla might not be a pelecypod, even though he considered Fordilla to

be a mollusk with two valves and he suggested the presence of a ligament. He was critical of Pojetaia as a pelecypod because he was not aware of a paper by Bruce Runnegar and Christopher Bentley (in press) describing the musculature of that genus. Yochelson (1981, p. 120) discussed the New Zealand species, but was not aware that D. I. MacKinnon's in-press paper on that taxon demonstrates that the species has foliated shell structure. Yochelson's concern about the stratigraphic gap between Fordilla and Tremadocian pelecypods is obviated by the new information. The total stratigraphic range of Fordilla, Pojetaia, and the New Zealand species is latest Tommotian or earliest Atdabanian to late Middle Cambrian (toward the upper limit of the Bolaspidella Zone). The possible pelecypod from Maryland is either late Franconian or Trempealeauan in age on the basis of conodonts. What we seem to be learning is that there was a radiation of Cambrian pelecypods, but that it took place at a small body size.

Pelecypods such as Fordilla and Pojetaia could be derived from rostroconchs such as Myona? queenslandica, which have a univalved protoconch, and at least some specimens of which have a flexible dorsal margin that could be interpreted as a ligament. The presence of such a margin implies a mechanism for closing the valves, adductor muscles.

#### CLASS SCAPHOPODA

Scaphopods are not yet known in Cambrian-age rocks, but the likely rostroconch ancestors of scaphopods occur in Late Cambrian-age rocks of Australia. The genus Pinnocaris has anterior and posterior shell gapes, an elongate body, no dorsal commissure, and the ventral sides of the valves touch at the commissure. It looks remarkably like a scaphopod and probably lived like one. The larval shell of Pinnocaris is near the anterior end of the conch, and growth is predominantly in a posterior direction. In scaphopods, all growth is directed anteriorly. Thus, Pinnocaris could not have evolved into a scaphopod by the simple fusion of the ventral margin. In rocks of Arenigian Age in Australia, some species of Pinnocaris become nasute anteriorly, and this trend continued in the genus at least until the early Caradocian. The oldest known scaphopod is Rhytidentalium from Shermanian-age rocks in Kentucky. It is postulated that scaphopods arose from rostroconchs by anterior elongation of the latter group (Pojeta and Runnegar, 1979).

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## 49. UPPER CAMBRIAN MOLLUSKS FROM THE ELLSWORTH MOUNTAINS WEST ANTARCTICA

By

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The Heritage Range of the Ellsworth Mountains of West (Lesser) Antarctica contains a sequence of Middle and Upper Cambrian rocks with a well-preserved and significant molluscan fauna in the Upper Cambrian part. In much of the rest of the world, many Late Cambrian mollusks are not well preserved. Most of the Cambrian mollusks from the Heritage Range are in metamorphosed, coarse, recrystallized, shelly packstone-wackestone carbonates which are loosely termed marbles. These carbonates are as much as 60 meters thick within a sequence of highly sheared argillites. The mollusks discussed herein are from the Minaret Formation, near the top of the Heritage Group, at one locality at the northern end of Webers Peaks on the east side of Springer Peak (lat. 79 deg., 22 min. S., long. 84 deg., 50 min. W.). The marble at this locality stands vertically, is as much as 18 meters thick, and is a coquina of trilobites and mollusks. Much less abundant in the fauna of the Springer Peak locality are archaeocyaths, echinoderm fragments, and articulate and inarticulate brachiopods. Mollusks are most abundant toward the top of the marble bed, and trilobites are abundant throughout the bed. The trilobites in the sequence are under study, but they are known to show Australian and Asiatic affinities. The agnostids and aphelaspids indicate a late Dresbachian age (early Late Cambrian). The mollusks suggest a slightly younger age, and the univalved forms are most like those described by Berkey (1898) from Franconian age rocks (middle Late Cambrian) in Wisconsin and Minnesota.

The environment in which the Springer Peak fauna lived is considered to have been shallow, marine, nearshore, and tropical. The tropical interpretation is based on many Late Cambrian-Early Ordovician reconstructions of Gondwanaland and on Antarctic paleomagnetic data. The fossil-bearing carbonate is a coquina representing an accumulation of wave or current-washed fossil debris. The archaeocyaths always occur broken and trilobites are disarticulated. The mollusks are well preserved, and most of them are present in growth series, suggesting that they may have lived at the site of accumulation.

The entire collection from Springer Peak is not yet fully prepared, but the mollusks known at present belong to the univalved classes Monoplacophora and Gastropoda and to the pseudobivalved class

Rostroconchia. Hyoliths also occur in this fauna, but the authors of this report disagree about the phylum to which this group of animals belongs. Of these four taxa, the monoplacophorans and gastropods are most abundant, and they occur in nearly equal numbers. The rostroconchs are least abundant and have been found only after intensive preparation of the sample in the laboratory.

### MONOPLACOPHORA

Several species of monoplacophorans are present in the fauna, including representatives of the genera Knighthoconus (Yochelson and others, 1973) and Proplina and others which in the most general ways are similar to Archinacella and Ozarkoconus. The most conspicuous monoplacophoran in the fauna is Knighthoconus that can reach a height of 50 mm. Proplina can reach a length of 50 mm, but is less abundant than Knighthoconus. The monoplacophorans include both low, cap-shaped forms and high, slightly curved conical species. The low forms have the characteristic elongate oval outline to the aperture. Most of the curved conical forms have a less elongate oval aperture, but in one group the aperture is nearly rectangular.

### GASTROPODA

There are at least four species of gastropods in the fauna, individual specimens of which range in size from 5 to 40 mm. One interesting aspect about the snails from this collection is that they are all "left-handed" in coiling when examined in standard orientation. It is difficult to decide whether gastropods are hyperstrophically coiled or sinistral, and this entire subject is a continuing source of debate. It is here noted that the Ellsworth Mountains Upper Cambrian gastropods are an unusual assemblage that is quite unlike assemblages known from the later Paleozoic.

An abundant gastropod at this locality is planorbiform in shape and somewhat similar to macluritaceans in gross aspect. However, the whorls just impinge on one another and the whorl profile is

oval rather than triangular.

A small trochiform species, possibly belonging to the genus Scaevogyra, is the most abundant gastropod. Some specimens of this species show raised colabral ridges, and the species may be allied to the rare genus Kobayashiella.

Less common in the collection are a moderately high-spired form that has a shape similar to that of the Silurian genus Onycochilus, and an even higher-spired species with moderately well-rounded whorls that may belong to the fairly well known genus Matherella. Matherella is widespread in rocks of Trempealeauan Age (late Late Cambrian) in North America.

#### ROSTROCONCHIA

The rostroconchs in the collection are all ribeirioids belonging to three genera. Like the trilobites, the rostroconchs show Australian and Asiatic affinities (Pojeta and others, 1977). The genus Wanwania is represented by one incomplete specimen, 11 mm long, that has the characteristic quadrate shape of some of the other species placed in this taxon. This may be the oldest known species of Wanwania, as elsewhere in the world the taxon is known from the Yingtzu Series and the Wanwankou Dolomite of northeast China, and the Ninmaroo Formation of Queensland, Australia, where conodonts indicate a late Datsonian age (early Early Ordovician).

A new species of Ribeiria, as much as 7 mm long, is known from seven specimens. It is most similar to R. australiensis that occurs in the Mungerebar Limestone of Queensland with trilobites that indicate a Mindyallan Age (early Late Cambrian).

There are 19 specimens, as much as 11 mm long, of a new species of the genus Apoptopegma. The Antarctic material is the oldest known occurrence of this genus. The only other known occurrence of Apoptopegma is in the Ninmaroo Formation of Queensland. In the Black Mountain section of Queensland, Apoptopegma occurs 15 m below the lowest known Datsonian conodonts and 41 m above the highest known Payntonian (late Late Cambrian) trilobites. The other mollusks associated with Apoptopegma at Black Mountain, and a second occurrence of the genus in the Ninmaroo Formation at another locality, suggest that in Australia Apoptopegma is Datsonian in age.

The Antarctic specimens of Apoptopegma differ from the Australian species in having a large, funnel-shaped anterodorsal aperture and a small slit-like

posterodorsal aperture. The Australian species have slit-like anterior and posterior shell gapes that extend along the greater length of those ends.

#### HYOLITHA

Hyoliths are represented in the fauna by three or four species assignable to the genera Hyolithes, Orthotheca, and Contitheca.

#### COMPARISON WITH OTHER ANTARCTIC LATE CAMBRIAN MOLLUSK FAUNAS

The only other known Antarctic Upper Cambrian molluscan fauna was reported from the Bowers Group in northern Victoria Land (Shergold and others, 1976), about 2600 km from the Ellsworth Mountains in East (Greater) Antarctica. Yochelson (in Shergold and others, 1976) described and discussed this fauna and identified the following genera: Scaevogyra, "Pelagiella", Hyolithes, and Contitheca. He suggested that Scaevogyra indicated a possible Trempealeauan Age (late Late Cambrian). The trilobites in the Bowers fauna indicate a latest Dresbachian age, approximately equivalent to the late Idamean Age of Australia.

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## 50. PALEOBIOLOGIC INTERPRETATION OF CAMBRIAN AND EARLIEST ORDOVICIAN CONODONT NATURAL ASSEMBLAGES

By

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In the past decade, many occurrences of conodont "natural assemblages" have been found, ranging in age from Cambrian to Triassic. These finds are important to conodont taxonomy because they can demonstrate the elemental makeup of multielement species. They also are important to conodont biology because they offer the best evidence for interpretations of shape and function of conodont apparatuses, and hence for interpretations and speculations concerning the affinities of conodontophorids with other groups.

Most recent discussion of conodont apparatus function has debated the mode of operation of the apparatus as a food-getting organ. Authors have centered their arguments on whether individual conodont elements acted as teeth (for example, Jeppsson, 1979; 1980), "superteeth" (for example, Landing, 1977; Tipnis and Chatterton, 1979), or tentacular supports in a lophophore (for example, Lindstrom, 1973; 1974; Conway Morris, 1976; 1980). We believe that available evidence indicates that many conodont elements formed parts of paired arrays of grasping or biting structures and that at least some protoconodonts are directly homologous with the grasping spines of chaetognaths.

### CAMBRIAN-ORDOVICIAN NATURAL ASSEMBLAGES

Although natural assemblages of oriented conodont elements were first reported nearly a half-century ago from Carboniferous black shales (Schmidt, 1934; Scott, 1934), the first report of an Ordovician natural assemblage was in 1967 (Barnes, 1967), and a report for the Cambrian was still later (Miller and Rushton, 1973). Natural assemblages of paraconodonts and Early Ordovician euconodonts were first reported by us recently (Szaniawski, 1980; Repetski, 1980) and this material comprises part of the basis for our interpretations.

The Cambrian and earliest Ordovician natural assemblages occur in two modes, as clusters of oriented elements on bedding plane surfaces or as fused clusters; that is, two or more elements are found physically joined at various points or areas. We are

considering as "natural" those assemblages whose constituent elements display an apparently nonrandom orientational relationship to each other. That is, the elements appear to occupy the appropriate positions as parts of size and or symmetry series produced by the conodontophorid, and are unlikely to be presently associated due to accumulation by for example, water currents or the alimentary processes of predators or scavengers.

Three types of elements, proto-, para-, and euconodont have been distinguished among the forms generally included within conodonta (see Bengtson, 1976). These types differ in their internal structure, a reflection of different modes of element formation, and in their ratio of organic matter to apatite, the proto- and paraconodonts having distinctly more organic matter relative to amount of apatite than do the euconodonts (Miller and Nogami, 1971). Proto- and para-conodonts generally are hollow cones with limited external complexity. Successive lamellae were added internally, so that element growth took place from the base. Paraconodonts have initially concentric lamellae, with later lamellae added internally and externally near the bases, but not continuous over the tip. Euconodont structure consists of concentric, externally serated lamellae, and each element can be divided into the highly apatitic conodont proper and the attached basal body. Bengtson (1976) concisely summarized current knowledge of conodont structure and his terminology is used herein; he developed the hypothesis then that early conodontophorid evolution led from proto- to para- and finally, in the Late Cambrian, to euconodont-bearing structures. The occurrence, then, of natural assemblages of all three types of conodont element in Upper Cambrian and lowest (-Tremadocian or lower Canadian) Ordovician rocks is especially fortunate because: (1) that was the only period when the three types coexisted, and (2) that was precisely the time during which the conodontophorids experienced their most dramatic evolutionary changes.

By far most of these older natural assemblages currently known involve the protoconodont "Prooneotodus" tenuis (Müller) (genus in quotes because type species of Prooneotodus is a paraconodont; see Landing, 1977). Miller and Rushton (1973) first

reported "P." tenuis assemblages, from bedding planes of Upper Cambrian black mudstones in cores from Great Britain. They determined that the apparatus consisted of two sets of parallel-oriented elements and that the sets were arranged symmetrically with concave edges facing each other. Müller and Andres (1976) then reported a 12-element bedding plane assemblage found in the Upper Cambrian black shales of Västergötland, Sweden. They noted that the elements of each set comprise a size series and proposed that the animal probably could add new elements to its apparatus during life. They also postulated that the "P." tenuis apparatus might have been a grasping organ and pointed out its striking similarity with the grasping structure of the modern chaetognath Sagitta, although they attributed this resemblance to convergence.

Discoveries of fused clusters of "P." tenuis (Landing, 1977; Tipnis and Chatterton, 1979; Abaimova, 1980; Repetski, 1980; Szaniawski, 1980, and in press) led to a clearer picture of the shape and structure of this apparatus, but also led to several different interpretations as to its function. Landing's (1977) material from the Upper Cambrian of New York State showed that the "P." tenuis apparatus consisted of two opposing "half-apparatuses," each having a crescentic cross section and bearing as many as 13 elements. The elements of each half-apparatus are situated lateral to each other and form a size series in which the medial elements are the longest. Landing (1977) proposed that the "P." tenuis had paired opposed half-apparatuses that functioned as pincer-like graspers, or "superteeth," the individual elements of each "supertooth" being juxtaposed along their length, and thus contributing to the strength of the entire unit. Tipnis and Chatterton (1979) described a cluster from the Upper Cambrian Road River Formation (slope-basin facies; Northwest Territories, Canada) that has two half-apparatuses preserved in the parallel-opposed position. They interpreted the structure as a grasping apparatus, following Landing (1977), but additionally suggested that the elements of each half-apparatus were fused during life. This led from their observation (Tipnis and Chatterton, 1979, p. 260) that the elements appeared to be constructed of inner and outer phosphate layers (separated by a gap that is as wide or wider than either layer), and that the outer layer of adjacent elements was fused in many cases. Element fusion during life would give additional strength for a grasping function, they said, and thus avoided the problem in Landing's model of slippage of adjacent elements.

Our studies of other fused cluster occurrences from Europe and North America led us independently (Repetski, 1980; Szaniawski, 1980) to the interpretation that the "P." tenuis apparatus was indeed probably a grasping apparatus, but that the individual elements were not laterally fused during the

animal's life. Comparative morphological and histological analysis shows that "P." tenuis apparatuses have such striking similarities to the grasping structures of modern chaetognaths that close biological relationship is indicated (Szaniawski, 1980, and in press). Paraconodont (Szaniawski, 1980) and euconodont (Repetski, 1980) clusters from this age interval are now known, and the interpretation of their apparatuses is consistent with a chaetognath model within the scenario of conodont element secretion developed by Bengtson (1976).

## THE CHAETOGNATH MODEL

Chaetognaths, a group of chiefly pelagic but also including benthic carnivorous marine invertebrates of phylum rank, have a grasping apparatus made up of two arrays of hollow chitinous spines and one or two sets of paired teeth (see Hyman, 1959, for comprehensive summary). The arrays of spines are paired symmetrically, and each has from 4 to 14 spines arranged in a crescentic shape. The spines are bared and are laterally discrete when in use for grasping prey; at rest the spines are laterally nested and are surrounded by a fold of soft tissue from the body wall, the hood. Each spine is held basally in a non-chitinous "socket."

Spines of some Holocene chaetognaths (for example, the geographically widespread genus Sagitta) are morphologically indistinguishable from well-preserved elements of "P." tenuis. Structurally, the fossil and Holocene spines also have in common a very thin outer layer that usually does not extend over the spine tip, a thicker lamellar middle layer that exhibits basal internal growth, and a very thin inner layer (Szaniawski, in press).

Compositionally, it is often difficult to determine primary from secondary phosphate in "P." tenuis, as well as in other fossils (Bengtson, 1976; Müller, 1979). However, most known "P." tenuis fused clusters are from geologic environments interpreted as deep, cool, and/or phosphate-rich; that is, environments conducive to precipitation of early diagenetic phosphate localized at sites of decaying organic matter (see Landing, 1977), and no clusters of the species are known among the reports of "P." tenuis from warmer, shallower environments that most likely had well-oxygenated bottom waters and bottom-dwelling scavengers. Under the chaetognath model, a dead "P." tenuis that settled onto a still, probably anoxic bottom, its grasping structure withdrawn into the hood, would be likely to have this apparatus preserved by very early post-mortem phosphatization of and epitaxial overgrowth (most likely also by phosphate) on the outer and inner spine layers. Merging of the outer layer overgrowths of adjacent elements produces a fused cluster. If the middle layer

should leach out later, then a gap between the inner and outer layers would be the result (see Tipnis and Chatterton, 1979, Pl. 29.1, figs. 7-9). Commonly the middle layer was mineralized, with the apatite crystallites re-oriented perpendicular to the wall, such as is seen in the Middle Cambrian protoconodont Hertzina? bisulcata Müller (Bengtson, 1976, p. 194 and fig. 5). Thicknesses of outer and inner layers of observed clusters are consistent for each cluster but vary a great deal between clusters, especially those from different localities. Further evidence that these phosphatic "crusts" are secondary, diagenetic products is a cluster having two oppositely-pointing half-apparatuses whose elements interfinger. The logical explanation for this interfingered orientation is the contraction between two sets of discrete elements upon death of the animal, and then fusion.

#### EUCONODONT CLUSTERS

Several euconodont fused clusters are known from earliest Ordovician phosphorites in Nevada (Repetski, 1980). They display the same laterally-juxtaposed orientation of elements seen in the protoconodont half-apparatuses. A three-element half-apparatus of Cordylodus lindstromi Druce and Jones also preserves the distal ends of oppositely pointing denticles that represent probably three elements belonging to the other half-apparatus of a pair. These clusters, and many others known now throughout the range of euconodonts (for example see Ramovs, 1978, for excellent Triassic examples), conform to the chaetognath-like grasping organ model if one takes into account the generally increased complexity of the younger apparatuses and the differences in mode of formation of euconodonts. Bengtson (1976) developed the hypothesis that in the evolution of euconodonts (from paraconodonts), the conodontophorid developed the ability to periodically have its elements enveloped by secretory tissue, hence allowing the construction of elements of much greater external complexity without radically altering the basic apparatus function. This periodic envelopment could have been by retraction of elements into epithelial pockets (Bengtson, 1976; Jeppsson, 1979), or, conversely, by modifications in a hood that gave some part of that organ the capability of secreting the elements.

Regardless of arguments of whether proto- and paraconodonts functioned as external or internal sclerites, the external mode of secretion of euconodonts requires that these elements were at least periodically enveloped by soft tissue. So, by their very occurrence as fused clusters in these rocks that also yielded "P." tenuis clusters, these euconodonts demonstrate that secondary phosphatization did in fact take place in these sediments. The secondary

phosphate appears in this instance as rough-textured surfaces in crevices, at points of contact, and along protected faces between adjacent, otherwise smooth, shiny-surfaced elements, and in the form of thin rods (of radially-oriented crystallites) that extend between elements. This diagenetic phosphate probably was localized at these protected sites of decaying sheets and strands of soft tissue.

#### GRASPING APPARATUS VERSUS LOPHOPHORE

Lindstrom (1973; 1974) and Conway Morris (1976) interpreted conodonts to be supporting structures in a lophophore. This interpretation requires that the elements be enveloped continuously in soft tissue. The structure of proto- and paraconodonts is more consistent with their functioning as exposed sclerites, and the periodic-envelopment model of Bengtson (1976) provides for continuity of this mode of function in the euconodonts. The Middle Cambrian species Odontogriphus omalus Conway Morris (1976) provides the most compelling evidence for the lophophorate interpretation. Unfortunately, the paraconodont-shaped sclerites that have been interpreted to lie in the bases of tentacles are now represented only by molds, and the question of whether these sites were originally occupied by conodonts or by some other cone-shaped sclerites must remain open pending discovery of more positive evidence.

#### CONCLUSION

Enough similarities exist between "Prooneotodus" tenuis and Holocene chaetognath grasping apparatuses (spine shape, morphology, and structure; apparatus construction) to warrant an interpretation that this protoconodontophorid probably was closely related to the Chaetognatha. Information from other protoconodonts and from paraconodonts is not conclusive at present, but is consistent with this interpretation. Euconodont apparatuses differed in complexity and element structure, but many of these also can be interpreted (and we believe are best interpreted) as grasping or biting structures, following Bengtson's (1976) and Jeppsson's (1979) model of periodic retraction-external function for euconodonts.

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## 51. TRILOBITE BIOSTRATIGRAPHY OF THE LOWER CAMBRIAN STAGES IN SIBERIA

By

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The principles of subdividing the Lower Cambrian into stages were established in the Cambrian stratotype section in England, where the succession of trilobite assemblages was ascertained and the *Olenellus* and *Protolenus* Zones were distinguished (Matthew, 1895). Yet the Cambrian System still has no internationally agreed-upon stages, and this circumstance encourages research workers from different countries to suggest regional schemes for subdivision into stages.

Evidence supporting a subdivision scheme for the Lower Cambrian of Siberia was presented in the publications of E. V. Lermontova (1951), N. P. Suvorova (1954) and N. V. Pokrovskaya (1954). On the proposal of F. G. Gurari and N. P. Suvorova (1954), the Aldan and Lena Stages were distinguished, and these have now come to be used in geological practice. Study of new materials has introduced several corrections into this scheme.

Three facies, each having its own particular type of section and fossil assemblage are roughly distinguished in the Lower Cambrian of Siberia (fig. 1). The Sinian-Botomian facies is rich in trilobites, and the section along the middle course of the Lena River is considered to be the stratotype for the Siberian Lower Cambrian and may be proposed as the stratotype for the stages of the Lower Cambrian Series (fig. 2).

The Lower Cambrian in Siberia is recognized by the majority of the research workers as the interval from the base of *Aldanocyathus sunnaginicus* Zone up to the base of *Schistocephalus antiquus* Zone.

Analysis of the trilobites from Siberia has allowed the author to conclude, that, if the Lower Cambrian is considered to have the above-mentioned extent, then three large trilobite associations can be recognized in all facies regions. On the basis of these trilobite associations and archaeocyathid assemblages, I. T. Zhuravleva, V. V. Khomevsky and I distinguished three stages (Repina and others, 1964).

It was thought that trilobites would not occur in lowest Lower Cambrian horizons, and this was one of the bases used to recognize the "pre-trilobite" Tommotian Stage. At the present time, however, trilobites are known from the lowermost Cambrian of the Aldan River (Fjodorov and others, 1979); they are not considered to represent an independent zone and

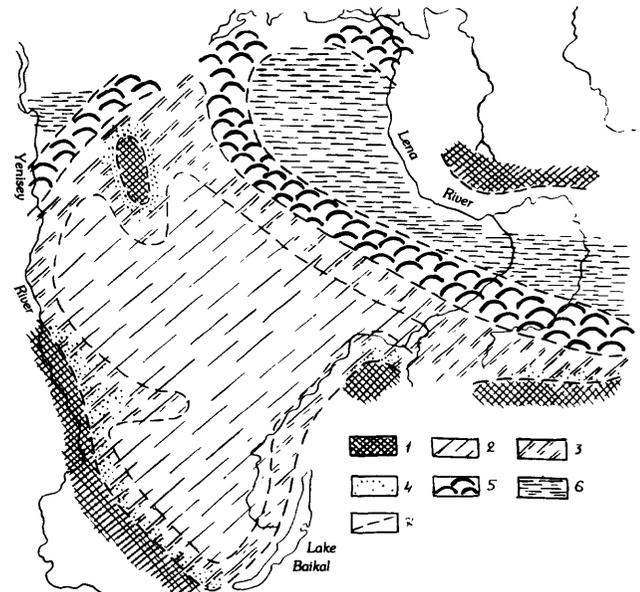


Figure 1.--Paleogeographic reconstructions showing various facies of the Siberian Platform during the Early Cambrian Epoch.

1, The land and archipelagoes of the islands. 2-4, Oljokma facies, salt-bearing basin of saline lagoon type: 2, central part of the basin with water of high salinity and deposition of dolomitic anhydrite and rock salt; 3, marginal zone of the basin with water of higher salinity and deposition of dolomitic, limestone-dolomitic, and rare calcareous sediments; 4, near-shore areas of salt-bearing basin with both terrigenous and carbonate sediments. 5, Sinian-Botomian facies, the zone of extremely shallow water of normal salinity, with deposition of calcareous, rare argillaceous-calcareous, and dolomitic-calcareous sediments. 6, Judomian-Olenek facies, shelf of open sea with water of normal salinity and of terrigenous and laminated carbonate sediments. 7, Supposed boundaries of facies.

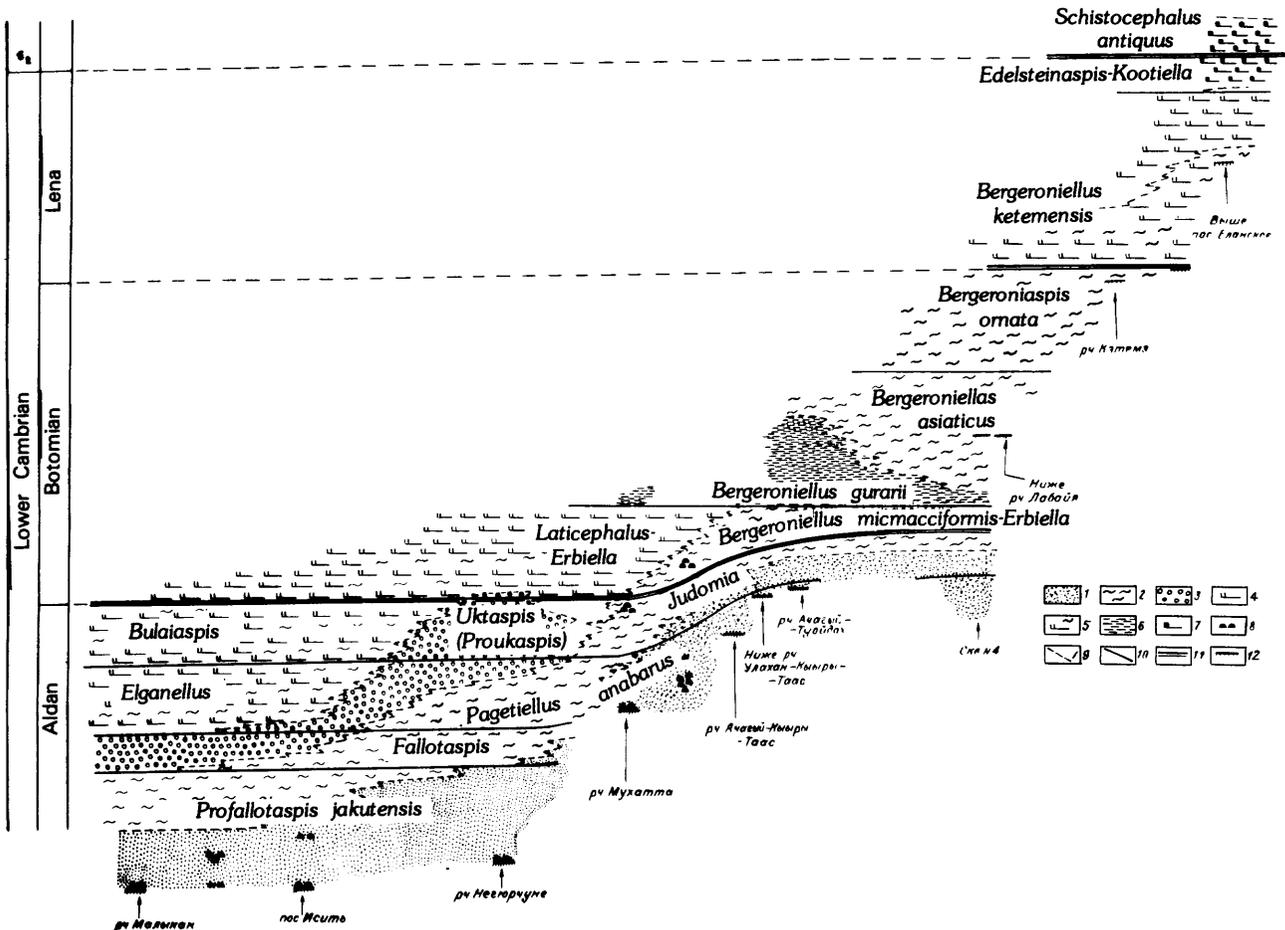


Figure 2.--Distribution of trilobite zones in the Lower Cambrian stratotype section of the middle course of the Lena River basin.

1, Deposits of variegated formation; 2, undulating-laminated and platy limestone, commonly dolomitic; 3, oolitic dolomite, rare limestone and dolomite with interbeds of oolitic dolomite; 4, dolomite; 5, dolomite with interbeds of limestone; 6, shale and thin-bedded limestone of the Sinian formation; 7, solid limestone of the Elanka formation; 8, bioherms; 9, boundaries of various facies; 10, boundaries of trilobite zones; 11, stages boundaries; 12, Lena River's water line in certain sections.

therefore cannot be used as the evidence for or against the independence of the Tommotian Stage.

The lowest stage with trilobites is the Aldan Stage. Until the question on independence of the Tommotian Stage is settled, the Aldan is recognized as the interval from the base of *Aldanocyathus sunnaginicus* Zone up to the base of the *Bergeroniellus micmacciformis-Erbiella* Zone. Its stratotype is located on the Aldan River, and its hypostratotype is along the Lena River, from the village of Isit' to the Sinei Creek. Trilobites of the suborder Olenellina and the family Pagetidae are characteristic of the Aldan Stage. On the basis of trilobites the following zones are recognized in the Lena section within the stage: *Profallotaspis jakutensis*, *Fallotaspis* (with the beds, possessing *F. explicata* and *F. sibirica*), *Pagetiellus anabarus* (with the beds possessing *Archaeaspis* and

*Nevadella*) and *Judomia* (figs. 3, 4). Characteristics of the Aldan Stage are present in all the sections of the type area. In the Oljokma facies region, representatives of the Neoredlichiidae family predominate in the Aldan Stage; olenellids are extremely rare. Two zones are distinguished: the *Elganellus* and *Bulaiaspis* Zones (see table 1).

The middle stage is the Botomian. It is recognized from the base of the *Bergeroniellus micmacciformis-Erbiella* Zone up to the *Bergeroniellus ketemensis* Zone. The stratotype of the stage is on the Botoma River. The hypostratotype is along the Lena River, from the Achchagyi-Kkyry-Taas Creek to the village of Botomai. The Botomian Stage is characterized by numerous Protolenidae and the representatives of other families. The following zones are recognized in the Lena sections within the stage:

Bergeroniellus micmacciformis-Erbiella, Bergeroniellus gurarii, Bergeroniellus asiaticus, and Bergeroniellus ornata (figs. 5, 6, 7). In the Judomian-Olenek facies, the deposits of this stage decrease in thickness. The zones of Caladiscus-Erbiella and Bergeroniellus expansus are commonly distinguished in this facies. Jakutiidae predominate in the Olekma facies, in which the Tungusella and Bathyriscellus robustus-Jakutus quadriceps Zones are distinguished.

The upper, or Lena Stage, includes the Bergeroniellus ketemensis and Kooteniella-Edelsteinaspis Zones (fig. 8). The stratotype of the stage is located in the Lena River basin, from the village of Tit-Ary to the village of Elanskoje. Representatives of the subfamilies Lermontoviinae and Paramicmaccinae and the superfamily Corynexochoidea are characteristic of the stage.

The subfamilies Lermontoviinae and Paramicmaccinae predominate in the Judomian-Olenek facies. The families Dolichometopidae and Namanoiidae predominate in the Oljokma facies.

The three stages distinguished in Siberia are well developed in various regions of the Soviet Union and in the sections of other countries. The principal difficulties that arise are related to differing interpretations of the extent of the Lower Cambrian in some countries.

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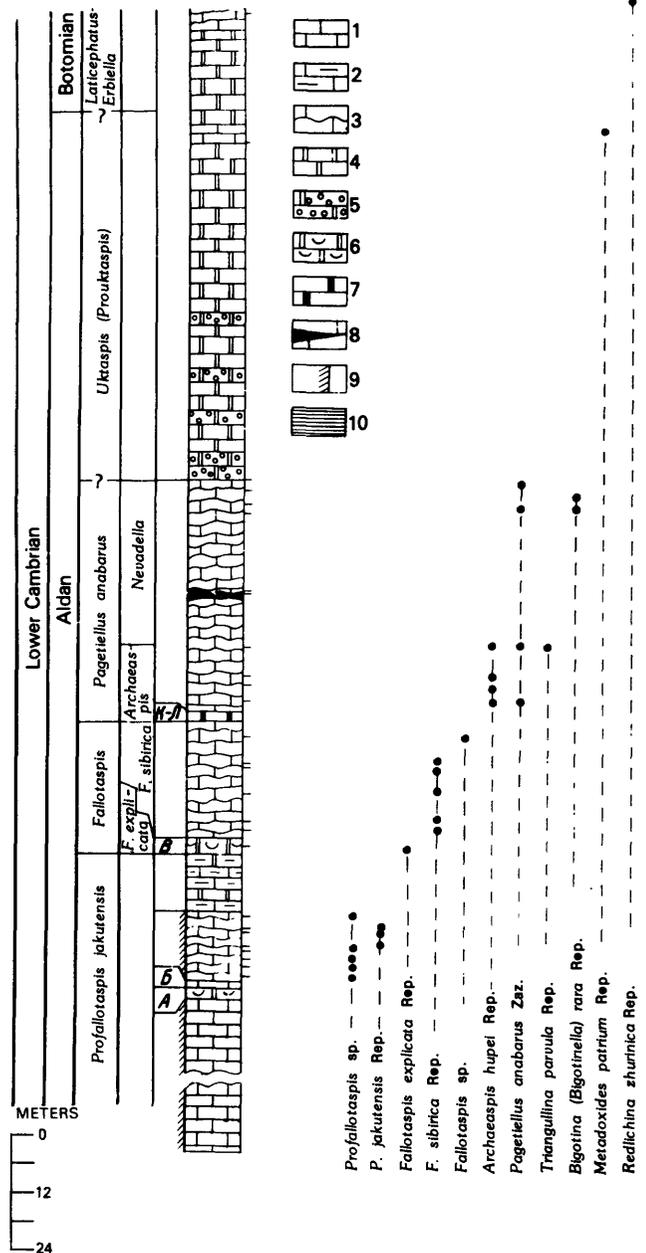


Figure 3.--Distribution of trilobites in the section of the right bank of the Lena River, opposite the mouth of the Negurchune River.

1, Limestone; 2, clayey limestone; 3, undulating-laminated limestone; 4, dolomite; 5, oolitic dolomite; 6, marker beds of dolomite and dolomitic limestone with shelly jointing; 7, solid light-colored limestone (marker bed "k-1"); 8, archaeocyathid bioherms; 9, variegated color of the rocks; 10, shale.

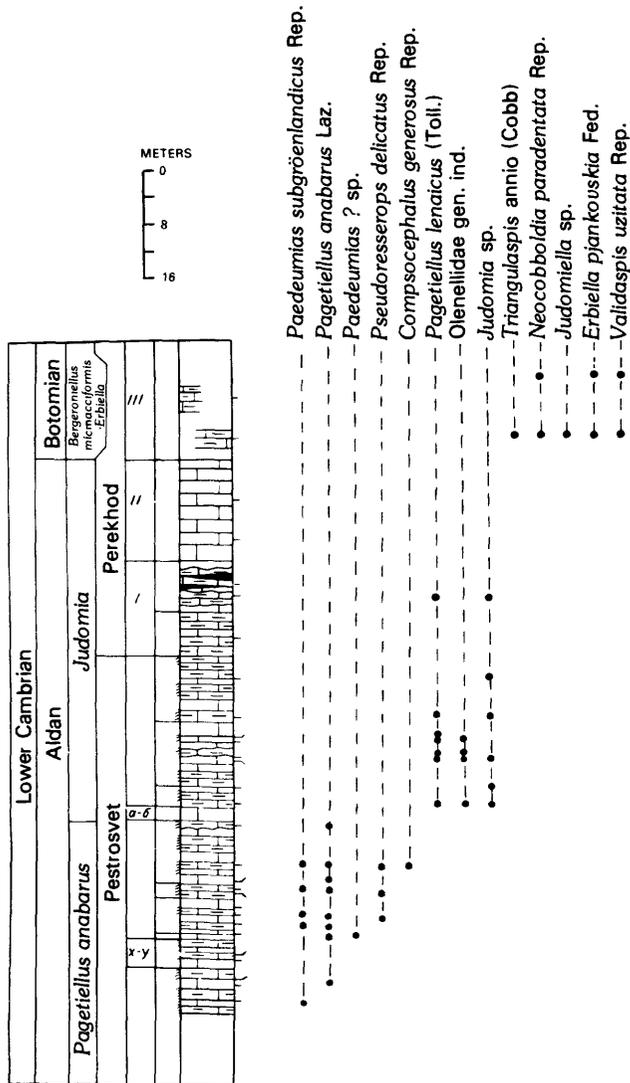


Figure 4.--Distribution of trilobites in the section of the right bank of the Lena River, near the mouth of the Achchagyi-Kyhyry-Taas Creek. Symbols as described in figure 3.

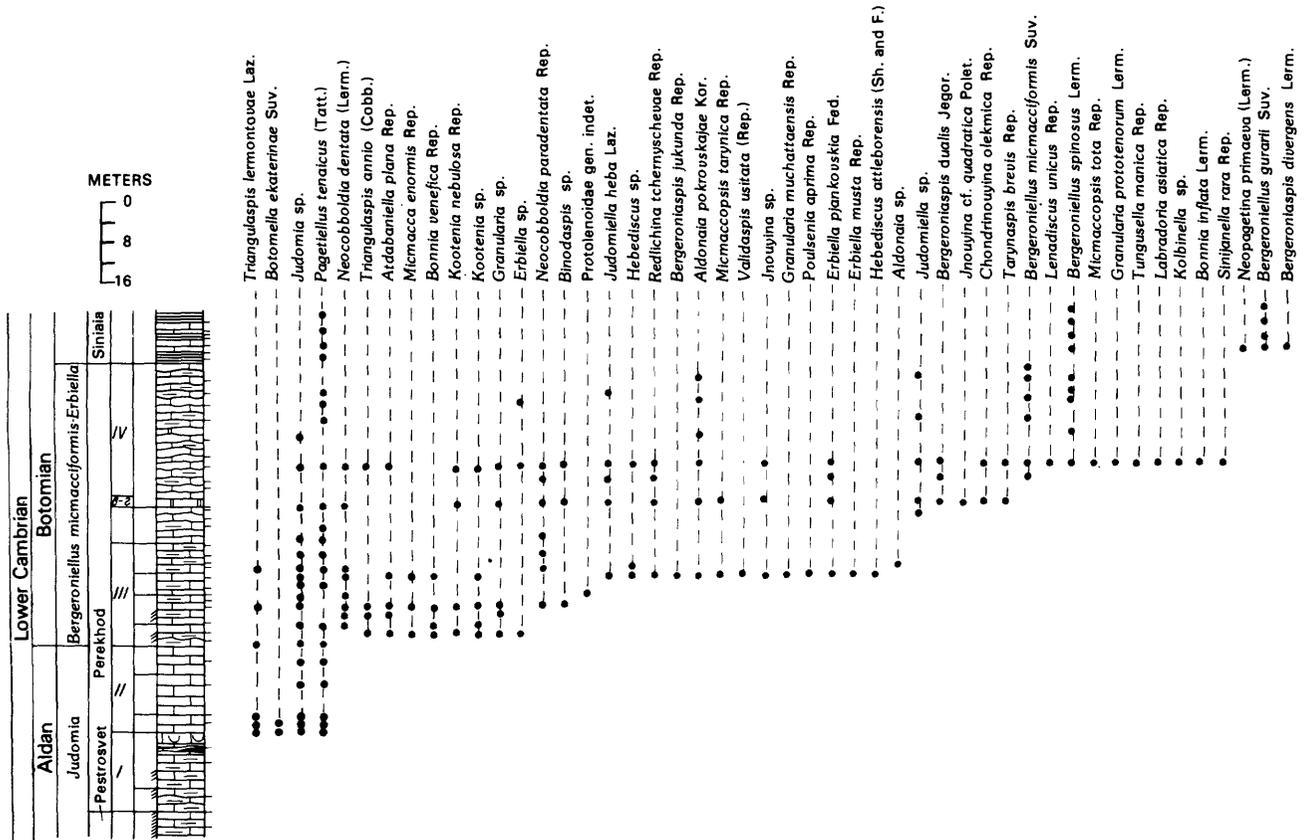


Figure 5.--Distribution of trilobites in the section of the right bank of the Lena River, 1.5 km below Ulakhan-Kyhyry-Taas Creek. Symbols as described in Figure 3.

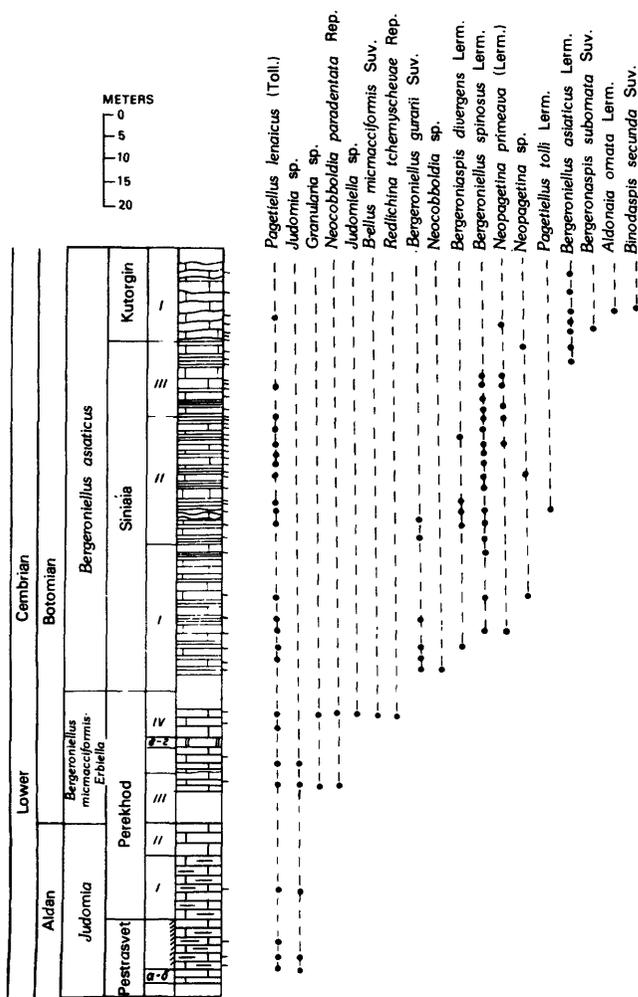


Figure 6.--Distribution of trilobites in the section of the right bank of the Lena River, 2.8 km below Achchagyi-Tuoidakh Creek. Symbols as described in figure 3.

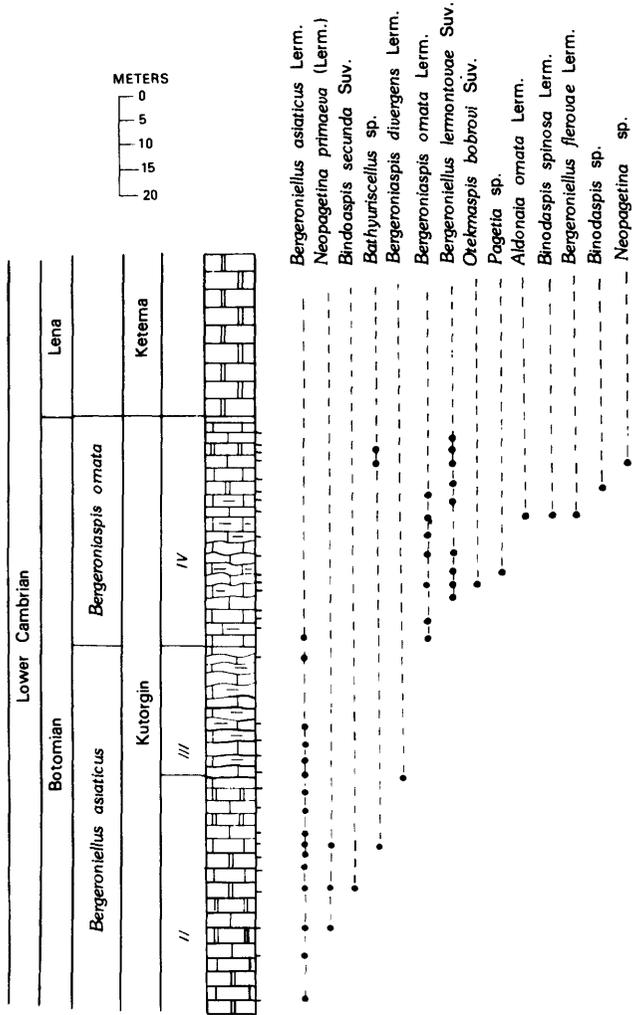


Figure 7.--Distribution of trilobites in the section of the right bank of the Lena River, 4 km below the Labaija Creek. Symbols as described in figure 3.



Stage	Oljokma facies region		Sinian-Botomian facies region			Judomian-Olenek facies region	Altai-Sayan folded region		
	Western type of section		Transitional type of section	Eastern type of section					
Lena	Namanian	<i>Namanoia</i>	<i>Laticephalus-Erbiella</i>	Elanka	<i>Edelsteinaspis-Kooteniella</i>	<i>Lermontoviella-Paramicmacca</i>	Obruchev	<i>Edelsteinaspis-Kooteniella</i>	
	Chara	<i>Parapoliella-Pseudoeteraspis</i>		Ketemenian	<i>Bergeroniellus ketemensis</i>		Solontsovsky	<i>Onchocephalina plana</i>	
Botomian	Olekma	<i>Bathyriscellus robustus-Jakutus quadriceps</i>			Sinian-Kutorginian	<i>Bergeroniellus asiaticus</i>	<i>Bergeroniellus expansus</i>	Sanashtykgol'sky	<i>Poliellina-Serrodiscus</i>
						<i>Bergeroniellus gurarii</i>			
	Uritsky	<i>Tungusella</i>			Tarynsky	<i>Bergeroniellus micmaciformis-Erbiella</i>	<i>Calodiscus-Erbiella</i>		
Aldan	Tolbachian	<i>Bulaiaspis</i>		<i>Uktaspis (Prouktaspis)</i>	Atdabanian	<i>Judomia</i>	<i>Judomia</i>	Kameshkovsky	<i>Sajanaspis</i>
	El'gianian	<i>Elganellus</i>	<i>Pagetiellus anabarus</i>	<i>Pagetiellus anabarus</i>				Bazaikhsy	<i>Resimopsis</i>
		?	<i>Fallotaspis</i>						
		<i>Profallotaspis jakutensis</i>							

Table 1.--Correlation of biostratigraphic schemes of the Lower Cambrian of the Siberian Platform based on trilobites from different facies.

## 52. CAMBRIAN SPONGES OF THE NORTH AMERICAN CORDILLERAN REGION

By

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Fossil sponges are widely reported from Cambrian and latest Precambrian rocks in the cordilleran region of western North America (fig. 1). Occurrences range from east-central Alaska (Allison, 1975) through western Canada and the western United States into the Oaxaca region of southern Mexico (Pantajo-Alor and Robison, 1967). In general, most reports of Cambrian sponges note only the occurrence of isolated spicules, principally of the relatively easily recognized 4- and 6-rayed spicules of the Hexactinellida. Second only to hexactine occurrences are those citing skeletal elements of the spongelike organism Chancelloria, are discussed later.

In spite of the widespread occurrence of spicules, articulated skeletons of sponges are relatively rare. Two of the most productive areas are the Burgess Shale, near Field, B.C., and the House Range in western Utah (fig. 1). The Burgess Shale suite is by far the most varied and those collections contain the best preserved Cambrian sponges known from North America. The Middle Cambrian Wheeler and Marjum Formations of Utah are a close second, however, not only in terms of numbers of total sponges recovered, but also in terms of preservation and variety.

Allison (1975) has illustrated a hexactine sponge spicule from the late Precambrian or possibly earliest Cambrian of east-central Alaska. These are certainly among the oldest hexactines recognized from North America. A. R. Palmer (in Finks, 1970, p. 6) concluded that the oldest hexactines known to that date in North America are Middle Cambrian, from the Bolaspis Zone. If the spicules from the Tindir Group of Alaska are dated properly, and there seems little question of their early age, they now extend the range of hexactine-bearing sponges considerably.

Slind and Perkins (1966) noted that "small sponges" occur in the Middle Cambrian Tatei and Chetang Formations between Jasper, Alberta, and Pine River, B.C. (loc. 2, fig. 1). They also noted Chancelloria from the same formation a few kilometers to the southeast. Chancelloria is one of the most widely reported Middle Cambrian sponges because of its distinctive spicules.

Locality 3 (fig. 1) is the Burgess Shale near Field, B.C. The sponges from there were described by Walcott (1920). Eighteen genera described by Walcott (1920) are known from the Burgess Shale and elsewhere, but 10 genera described in his classic study

are known only from that locality.

Norris and Price (1966, p. 392) reported Chancelloria from the Gordon Formation east of Cranbrook, B. C. (loc. 4, fig. 1).

Lochman (1950) discussed Cambrian faunas from the Little Rocky Mountains of central Montana (loc. 5, fig. 1) and reported a large number of hexactine-based sponge spicules from argillaceous rocks of the Upper Cambrian Pilgrim Formation. She tentatively assigned these spicules to Protospongia, an assignment that seemed appropriate at that time. We now know that stauractine and hexactine spicules occur in several genera in the Protospongioidea and that identification of generalized isolated spicules is not reliable.

Isolated hexactines from the Upper Cambrian Snowy Range Formation (loc 6, fig. 1) were identified by Grant (1965) as Multivasculatus. He noted that hexactines are a good local guide to Trempealeauan rocks and are rare in Franconian units.

The articulated hexactinellid sponge Multivasculatus was described from the Upper Cambrian Gallatin Limestone in the Big Horn Mountains (loc. 7, fig. 1) by Howell and Van Houten (1940). This specimen and another figured by Finks (1970) from near Eureka, Nevada are the oldest known articulated thick-walled hexactinellid sponges.

Okulitch and Bell (1955) described Gallatinospongia from the Upper Cambrian Gallatin Limestone of the Wind River Mountains (loc. 8, fig. 1). Gallatinospongia could have given rise to the abundant anthaspidellid sponges of Ordovician and younger rocks.

Rigby (1980) described a large Vauxia from the Middle Cambrian Spence Shale Member of the Lead Bell Shale in northeastern Utah (loc. 9, fig. 1). Locality 10 is from the Toiyabe Range, north-northeast of Austin, Nevada, where Diagoniella cyathiformis occurs at locality 17 of Stewart and Palmer (1967, p. D58).

Locality 11 is the Eureka district of Nevada where Middle Cambrian Protospongia fenestrata Salter was cited by Walcott (1886) and Hague (1892).

Locality 12 is the House Range area where a fair variety of Cambrian sponges have been collected. Walcott (1920), Robison (1964), and Rigby (1966, 1969, 1978), Rigby and Gutschick (1976) have described the sponge faunas from there.

Locality 13 marks the occurrence of spicules provisionally identified as Tholiasterella by Resser

(1945), who figured and briefly described the sponges that were also noted by McKee (1945).

Lochman (1952) noted *Chancelloria* from the Middle Cambrian Arrojos Formation from near Caborca, in northwestern Mexico (loc. 14).

Pantoja-Alor and Robison (1967) listed an abundant fauna from the basal Paleozoic formation in the Nochixtlan area of Oaxaca. Sponges are associated with other fossils in an assemblage indicative of latest Cambrian to earliest Ordovician age (loc. 15).

These are localities for which specific references are made to genera or types of sponges. Innumerable other localities could also be listed where isolated sponge spicules or spiculites play an important part in the section. Early protosponges were probably very common elements in deeper quiet waters in both the outer carbonate and clastic facies on the western margin of North America.

Now let us examine a few genera of Cambrian fossils. *Chancelloria* was considered as a stem sponge of the heteractinids (Rigby and Nitecki, 1975). *Chancelloria* (Walcott, 1920; Rigby, 1978) is a subcylindrical form, armored with several ranks of large, hollow-rayed, spicules or rosettes. *Chancelloria* may have secreted a skeleton over an exceedingly large organic fiber, but chemical makeup of the hollow ray, the ray perforation, and the suturing of individual elements to produce the rosettes all seem unspongelike. *Chancelloria* is currently under study. It probably does not belong within the Porifera.

Most isolated stauracts or hexactine-based spicules have traditionally been identified as from *Protospongia*. However, *Diagoniella*, among others, also contains these same kinds of spicules, and locally *Diagoniella* is considerably more common (Rigby, 1978). Many well-preserved spicules of *Diagoniella* show minute longitudinal ribs, thus allowing differentiation of at least those spicules from smooth unstratified ones of *Protospongia*, even when isolated.

*Leptomitus* (= *Tuponia*, Walcott, 1920) has been viewed as having a thin wall made of nearly vertical to gently spiraling long spicules. New, virtually complete specimens of *Hintzespongia* (Rigby and Gutschick, 1976) have a thin spongocoel filling and clearly show a two-layered wall and that the regularly quadrated layer of stauracts is the outer one. In addition, outer spicules are oriented diagonal to the principal axis of the thistle-funnellike small sponge. An additional new double-walled Middle Cambrian protosponge has been recovered from the House Range. It is more test tube-shaped and has a considerably finer skeleton than *Hintzespongia*.

The occurrence of several Middle Cambrian genera having mixed regular and irregular double walls reinforces the idea that the later dictyosponges perhaps developed from forms having a regularly oriented dermal skeleton, whereas the later brachiosponges may have had an origin from those that had an irregular internal skeleton. These fossils and those described by Walcott from the Burgess Shale are presently under study as part of a major review of Cambrian sponges of North America.

This research has been supported by a grant from the National Science Foundation.

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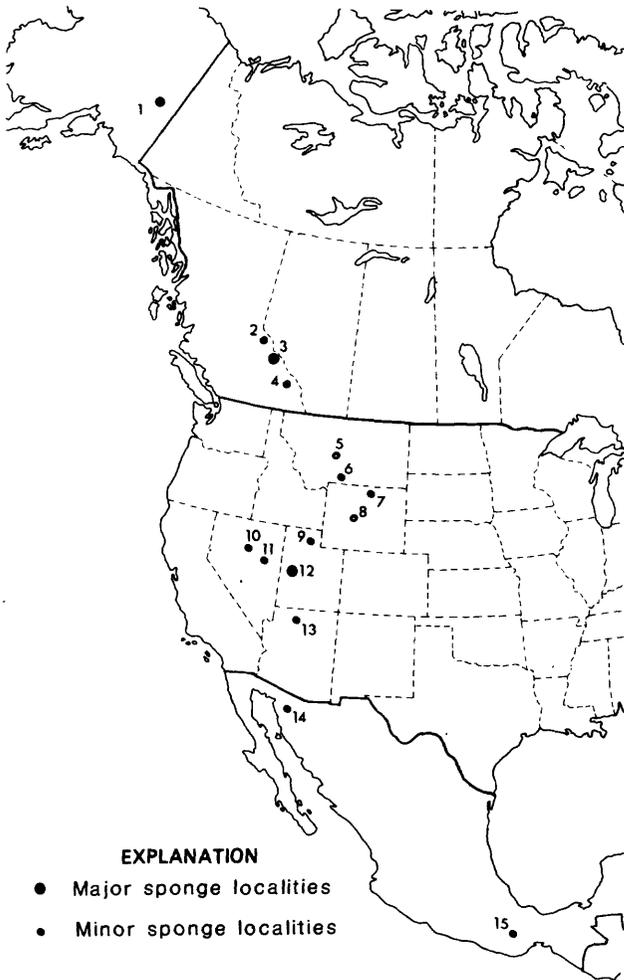


Figure 1.--Index map showing Cambrian sponge localities, in the western cordillera of North America.

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### 53. THE CAMBRIAN BRACHIOPOD RADIATION-- MONOPHYLETIC OR POLYPHYLETIC ORIGINS?

By

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The traditional view of brachiopods is that they form a monophyletic phylum (Williams and Rowell, 1965; Williams and Hurst, 1977) whose closest relatives are the other lophophorates, the phoronid worms and bryozoans. It is commonly accepted that these lophophorates radiated from a trimerous, tubicolous coelomate ancestor (Clark, 1979), but there are some problems in fitting the ectoproct bryozoans into this phylogenetic hypothesis (Nielson, 1977).

In contrast, brachiopods are a grade of organization, not a clade, according to Cowen and Valentine (in Valentine, 1973). Although they accepted the conventional view of the monophyletic nature of the articulate, they argued that these forms originated along a different adaptive pathway from the inarticulate. Furthermore, they asserted that the various inarticulate lineages may themselves have followed different pathways from an ancestral phoronid-like worm. In Cowen and Valentine's view, the brachiopods are polyphyletic and the nearest common ancestor of the various brachiopod stocks was a phoronid-like coelomate, not a brachiopod. As a corollary, they claimed that several monophyletic phyla would be needed to classify the organisms presently called brachiopods.

Wright's (1979) view of brachiopod phylogeny was similar to that of Cowen and Valentine, differing primarily in postulating a lingulide ancestry for the articulate. Wright considered that brachiopods may have originated in as many as seven different lineages from separate brachiophorate stocks. The latter were defined (Wright, 1979, p. 238) as, "...infaunal lophophorate stocks with the potential to develop into epifaunal brachiopods." They were shown (Wright, 1979, fig. 1) as infaunal wormlike creatures with lophophores projecting freely from their tubes.

The principal objectives of this contribution are to analyze these competing hypotheses, ascertain what characters corroborate each hypothesis, and, insofar as possible, determine whether brachiopods had a monophyletic or polyphyletic origin.

#### TAXONOMIC METHODS AND PHYLOGENY

The traditional paleontological approach to phylogeny construction is based on an assessment of similarity between taxa after eliminating the effects of convergence. To greater or lesser extent, stratigraphic and geographic data are considered prior to making the inferred phylogenetic tree and functional considerations may have entered into its construction. Although this approach is not without its critics, our understanding of the evolution of most fossil invertebrate groups is based largely on such a method.

Previous attempts at unravelling the early phylogenetic history of brachiopods have followed this tradition. They encounter, however, two difficulties. Brachiopods from the Tommotian Stage, usually regarded as lowest Lower Cambrian, are very poorly known. Lower Tommotian rocks are commonly almost unfossiliferous and their brachiopods have been described only from Siberia (Pelman, 1977). Even brachiopods from the overlying Atdabanian Stage are known in some detail only from two regions (Pelman, 1977; Rowell, 1977). Secondly, if one is prepared to concede that brachiopods may have diversified initially as soft-bodied animals, or forms whose mantles secreted only organic material (as Wright, 1979 maintained), then first appearance in the fossil record reveals nothing of ancestor-descendant relationships. Such appearance at best marks the time at which the lineage developed the ability to secrete calcium carbonate or calcium phosphate. Consequently, earlier endeavors to understand the initial brachiopod radiation, including my own, had to rely solely on morphological comparison between Cambrian taxa that may have had a significant evolutionary history prior to developing a mineralized shell. The usual paleontological constraints in making a phylogenetic tree, stratigraphic position and homotaxial sequence, simply are not available. Statements regarding the monophyletic or polyphyletic origin of brachiopods thus represent little more than the author's subjective assessment of the significance and degree of similarity perceived between representatives of Cambrian brachiopod orders. If we are to make progress towards

understanding the initial brachiopod radiation, a different approach to analyzing our information is needed. Fortunately appropriate techniques are available.

Cladistic taxonomic methods are designed to analyze genealogical relationships among taxa, the branching pattern of evolution. Such methods are not new (Henning, 1966), but only within the last few years have paleontological audiences have been widely exposed to them (for example, Eldredge, 1979). Unfortunately these methods have their own formidable jargon, but it is trivial in comparison with that associated with the morphological description of any major group of organisms. Page limitations preclude discussing these techniques in detail, but comprehensive accounts are available (Eldredge and Cracraft, 1980). In essence, these methods recognize that when the effects of superficial resemblance due to convergence are removed, two types of evolutionary similarity are possible, and they are of unequal importance in terms of deducing phylogenetic relationship. At any given level of analysis, the resemblance between two taxa may be due to "...shared evolutionary novelties inherited from an immediate common ancestor and thus not to be found in any other taxon...." (Eldredge, 1979, p. 167). Such similarities are termed synapomorphies and they are in contrast to symplesiomorphies, which are similarities inherited from some more remote common ancestor that may be found also in other descendant taxa. Only synapomorphies, the joint possession of new innovations, provide information on the close phylogenetic relationship between two taxa. Thus, whereas study of all available characters is needed to evaluate the total evolutionary history of a group of organisms, only some of the observed similarities, the synapomorphous ones, provide information on its cladistic or phylogenetic history. This principle seems to be increasingly accepted in systematic theory and practice (Ashlock, 1979).

The inferred phylogenetic relationships are commonly expressed as cladograms, branching diagrams showing the nested pattern of synapomorphy distribution. A cladogram is not a phylogenetic tree, yet a cladogram may be derived from a tree. Without making further assumptions, the only cladistic information deducible from a cladogram is that two taxa united at a node share a common ancestor not shared by other taxa under consideration (Eldredge, 1979, p. 169). Figure 1 is a partial cladogram that may be derived from Wright's (1979, fig. 1) partial phylogenetic tree. It may be compared with other cladograms produced directly from consideration of the distribution of synapomorphy among brachiopods (figs. 2 and 3).

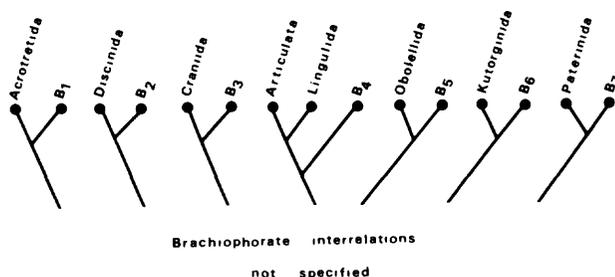


Figure 1.--Partial cladogram derived from Wright's (1979, fig. 1) phylogenetic tree. B<sub>1</sub>-B<sub>7</sub> are seven different brachiophorates shown by Wright as tubicolous, phoronid-like worms.

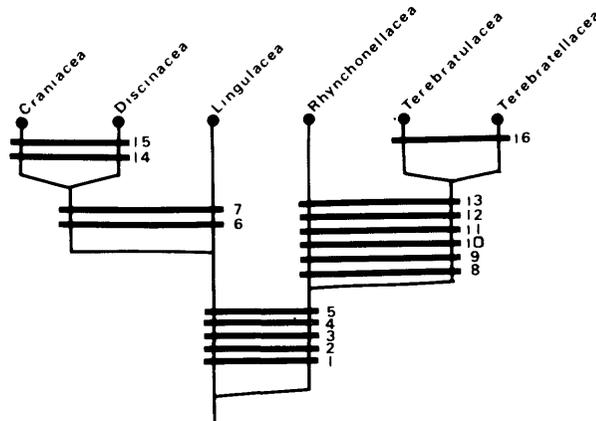


Figure 2.--Cladogram showing relationship between major taxa of extant brachiopods. Synapomorphies, uniquely derived characters, shown by bars connecting taxa are: (1) mantle canals, (2) generative zone separating inner and outer mantle epithelium, (3) double row of filaments on adult lophophore, (4) brachial lip bounding brachial groove, (5) two mesocoelic cavities in lophophore, (6) hydraulic mechanism for opening valves, (7) presence of larval shell, (8) diductor muscles and hinge mechanism, (9) posterior fusion of mantles, (10) fibrous secondary shell, (11) pedicle as larval rudiment, (12) mantle reversal during larval life, (14) closely comparable oblique internal and oblique lateral muscle paths, (15) holoperipheral growth in both valves, (16) presence of loop.

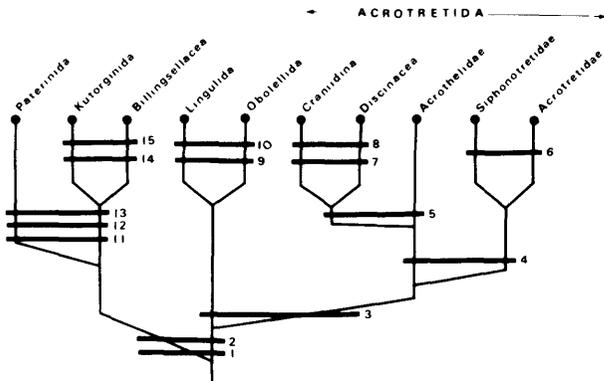


Figure 3.--Cladogram showing relationship between principal major taxa of Cambrian brachiopods. (The Craniidina and Discinacea are first recorded in the Lower Ordovician, but are included to complete major coverage of the Acrotretida.) Synapomorphies, uniquely derived characters, shown by bars connecting taxa are: (1) secretory activity of outer epithelium of both mantles, (2) development of setae at mantle margin, (3) peripheral location of shell muscles in body cavity, (4) holoperipheral growth in ventral valve, (5) flat or gently conical ventral valve, (6) similar structure of dorsal pseudointerarea, (7) subequal anterior and posterior adductor muscle scars, (8) oblique internal and oblique lateral muscles, (9) large anterior adductors, (10) marginal beak in both valves, (11) medially located muscle scars, (12) straight posterior margin of shell, (13) open delthyrium, may be partially closed apically, (14) pseudodeltidium, (15) apical pedicle foramen.

#### DISTRIBUTION OF SHARED SYNAPOMORPHIES AMONG BRACHIOPODS

In using the cladistic methods, it is clearly important to recognize correctly similarities that are due to synapomorphy, the joint possession of a uniquely derived character. This may be relatively easy for some characters but virtually impossible for others. Outgroup comparison and ontogenetic studies may be helpful in reaching a decision (Eldredge and Cracraft, 1980). For example, in figure 2, character 1, the presence of mantle canals is shown as a derived character that unites the principal taxa of living brachiopods. This feature is regarded as a synapomorphy by outgroup comparison with other

lophophorates, for example, the phoronids. Mantle canals are found in all living brachiopods; indeed, to judge from shell impressions they were a feature of all fossil forms. They are unknown in other lophophorates and the inference is that their universal presence in brachiopods represents inheritance from a joint common ancestor. The same argument may be applied for characters 2 through 5 of figure 2. These four characters support the hypothesis that living brachiopods shared a common ancestry distinct from that of other lophophorate groups.

Characters 6 and 7 of figure 2, hydraulic mechanism for opening the valves and the presence of a larval shell, provide examples of characters that are more difficult to analyze. They are shown as derived features that unite the inarticulates. It is also possible to argue that they were primitive plesiomorphic features at this level and should be shown as additional features uniting all brachiopods. With this interpretation, the absence of these features in living articulates would be a derived condition supporting characters 8 through 13, and reinforcing the contention that the articulates are a monophyletic group.

As will be apparent, one of the advantages of cladistic methods in studying the nature of the origin of brachiopods is that attention does not have to be limited to only Cambrian taxa. Under appropriate circumstances, information from the soft tissue of living forms may be combined with data from fossil representatives. Figure 3 is a cladogram that includes the principal groups of Cambrian brachiopods. It is clearly comparable with that of figure 2, which is concerned with only living taxa. The latter is based on a number of features that are not preserved in fossils, but suffers from the obvious limitation of not considering the extinct Paterinida, Kutorginida, and Articulata. The two cladograms complement each other.

#### CONCLUSIONS

If features (1) through (5) of figure 2 are derived evolutionary novelties for all extant Lingulida, Acrotretida, and Articulata, then it follows from the form of the cladogram of Cambrian brachiopods (fig. 3) that they are derived features for all brachiopods. Thus, joint consideration of both cladograms shows that a monophyletic origin for the brachiopods is supported by a minimum of seven characters that are synapomorphous, the five mentioned above and characters (1) and (2) of figure 3. These seven characters include development of dorsal and ventral mantles, the presence of marginal setae, and details of mantle and lophophore structure

The distribution of these seven characters is not consistent with the interpretation that brachiopods have developed along separate pathways from

different phoronid-like ancestors. The only alternative explanation is that these similarities are not homologous but merely examples of convergent evolution; this seems unlikely and certainly is not a parsimonious solution. Furthermore, there are no known synapomorphies to support a polyphyletic origin for the brachiopod. I am unaware of any feature that is found only in some phoronids and some brachiopods.

I conclude that brachiopods are a monophyletic group that are best treated as a distinct phylum because of their morphological homogeneity. Paradoxically, Wright (*in* House, 1979) made the same statement. If this is his considered opinion, I can infer only that he "misdrew" himself in illustrating brachiophorates (1979, fig. 1). Our general views can be reconciled by regarding brachiophorates as brachiopods. It is certainly possible, even probable, that some brachiopod lineages differentiated prior to acquisition of a mineralized shell. If so, development of a mineralized shell is an example of convergence within the group. Terms like monophyly and polyphyly, however, are defined by group relationships, not level of development of one or more characters (Patterson, 1978). Consequently, these shell-less organisms were brachiopods, not phoronid-like worms. The concept of a polyphyletic origin for Cambrian brachiopods is an interesting speculation, but there is seemingly no evidence to support it.

Development of ideas expressed here has occurred over several years during which I have been supported by National Science Foundation grants DES 75-21499 and EAR 79-19973. I thank my colleague E. O. Wiley for clarifying some of my thoughts, the remaining heresies are mine.

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## 54. BASINAL DEPOSITS AND OUTER SHELF BASINS, IN THE CAMBRIAN OF NEVADA AND UTAH

By

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Although shallow subtidal and peritidal carbonates have attracted considerable attention in the Cambrian of the Great Basin, only recently have deeper water basinal rocks been the focus of study (Taylor and Cook, 1976; Cook and Taylor, 1977; Rowell and others, 1979; Cook, 1979; Brady and Koepnick, 1979; Rees and Rowell, 1980).

The basinal deposits have a modest variety of lithofacies but invariably include parallel laminated shale. Hemipelagic sediments occur but many are gravity-flow deposits. Characteristically such rocks are either unfossiliferous or yield a low-diversity fauna dominated by pelagic agnostoid trilobites, suggesting that many of them were deposited under anoxic conditions. But, from time to time, bottom conditions improved sufficiently for benthic organisms to flourish.

Mapping the geographical and temporal distribution of basinal facies across Nevada and Utah provides insight into changing paleotopography. The results are shown in figures 1-4 plotted on a nonpalinspastic base that differs only modestly from available palinspastic reconstruction for strata beneath the Roberts Mountains thrust (Stewart, 1980). Details of original basin shape have been modified by subsequent tectonic movement, but we consider that the broad relationships have been preserved. The pattern of distribution of basinal facies is more complex than previously appreciated, particularly in Upper Cambrian strata. Some of the basins were ephemeral; these clearly were situated on the continental shelf. The location of other basinal deposits relative to the Cambrian continental shelf-slope break is more enigmatic.

### EVOLUTION OF THE OUTER SHELF BASINS

All known autochthonous or parautochthonous Cambrian basinal rocks of Nevada and Utah accumulated in regions that are underlain by shallow-water rocks of the upper Precambrian and Lower Cambrian clastic wedge. Seemingly these latter sediments rapidly blanketed any relief associated with late Precambrian rifting events (Stewart, 1972), and no deep-water rocks of this age are known.

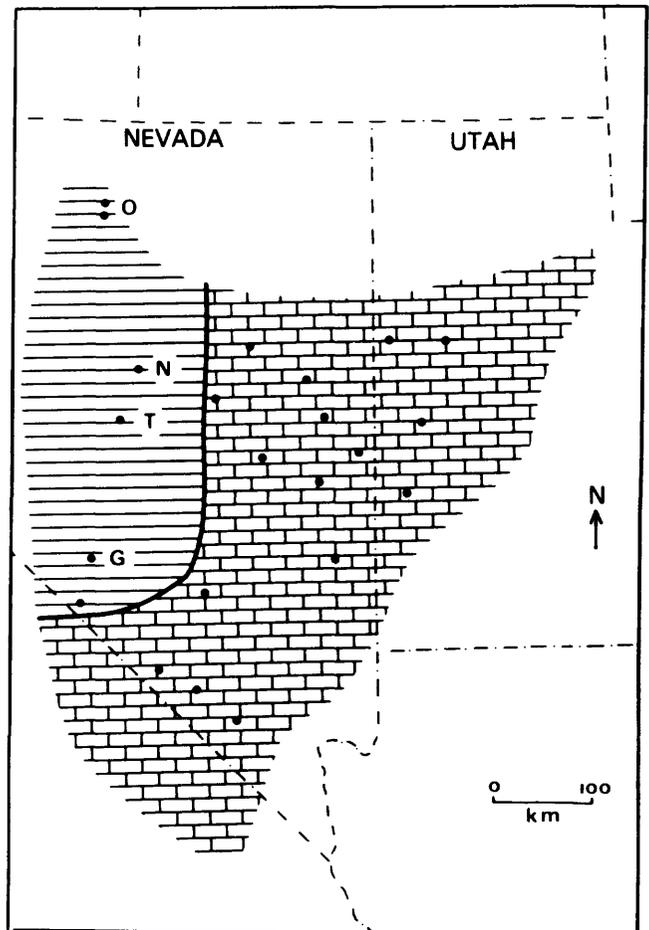


Figure 1.--Nonpalinspastic map of distribution of basinal facies (horizontal lines) and bounding subtidal and peritidal facies (brick pattern) in the Middle Cambrian immediately prior to the *Ptychagnostus gibbus* Chron. Dots show control localities. Geographic locations mentioned in text: O, Osgood Mountains; N, northern Toiyabe Range; T, southern Toiyabe Range; G, Goldfield.

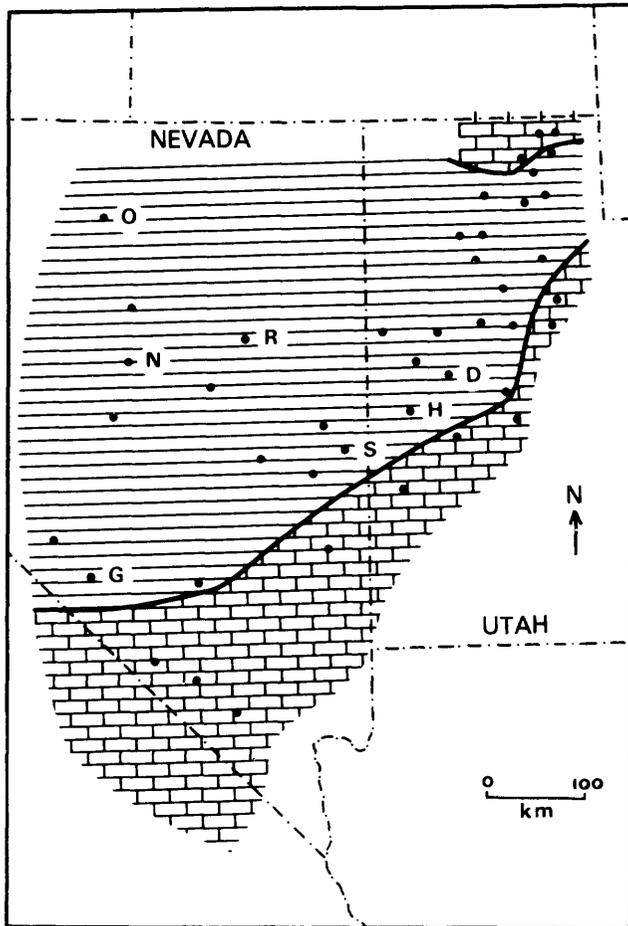


Figure 2.--Nonpalinspastic map of distribution of basal facies (horizontal lines) and bounding subtidal and peritidal facies (brick pattern) in Middle Cambrian *Ptychagnostus gibbus* Chron. Localities mentioned in text: O, Osgood Mountains; N, northern Toiyabe Range; G, Goldfield; R, Ruby Range; S, Snake Range; H, House Range; D, Drum Mountains. Data at most control points (dots) is from R. A. Robison, (personal commun., 1980).

the sequence of carbonate turbidites and debris-flow deposits of the Preble Formation in the Osgood Mountains (fig. 1; Rowell and others, 1979; Rees and Rowell, 1980) is contemporaneous with shoal-water carbonate to the east. Indeed some of the shallow-water carbonate clasts in the debris flows may have been derived from this shoal area. To the south of the Osgood Mountains, in the Toiyabe Range, relief may have been less, for coarse-grained gravity-flow deposits of this age are unknown.

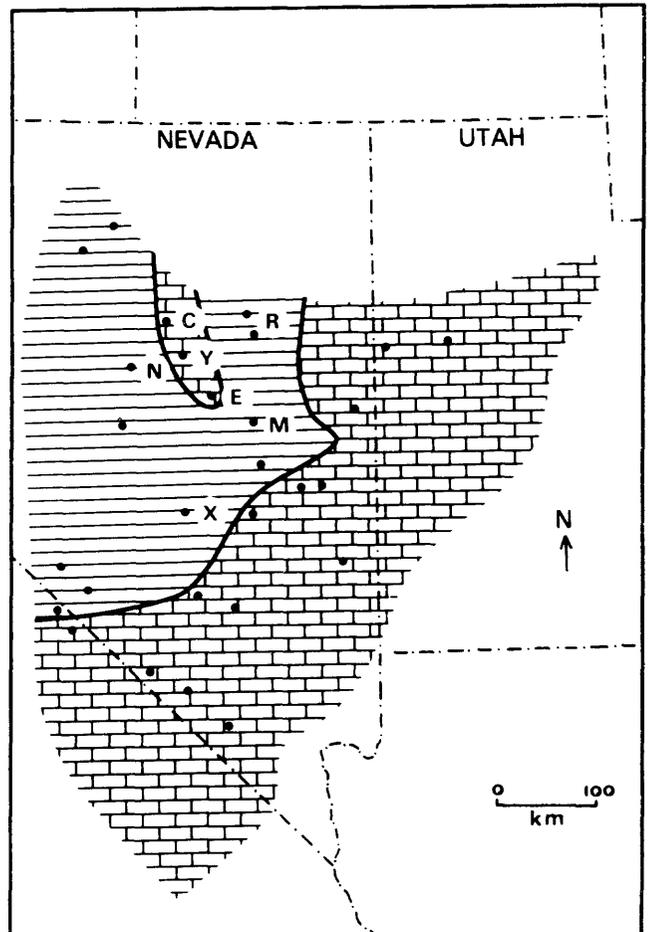


Figure 3.--Nonpalinspastic map of distribution of basal facies (horizontal lines) and bounding subtidal and peritidal facies (brick pattern) in Late Cambrian (middle Dresbachian, early *Aphelaspis* Chron). Localities mentioned in text: N, northern Toiyabe Range; C, Cortez; Y, Roberts Mountains; E, Eureka; R, Ruby Range; M, Mount Hamilton; X, Hot Creek Range. Dots show control localities.

Although shallow subtidal and peritidal sediments were deposited over much of the Great Basin in early Middle Cambrian time (fig. 1; Palmer, 1971), differential subsidence and sedimentation allowed deeper water sediments to accumulate in the more westerly regions of the present Cambrian outcrop belt. These deposits are represented by parts of the Broad Canyon and Crane Canyon sequences and parts of the Emigrant and Preble Formations. Faunal control in these beds is poor, but seemingly some of

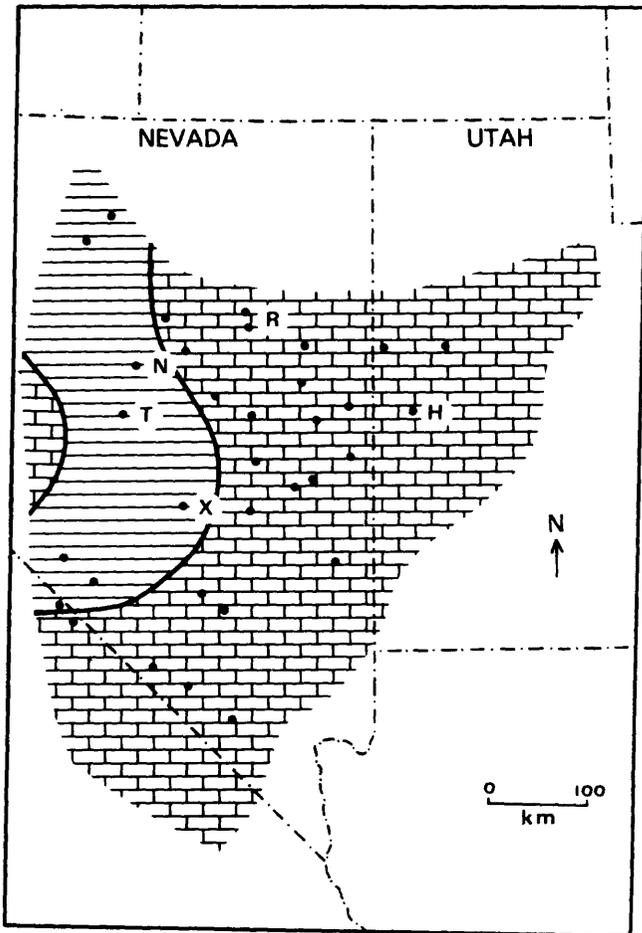


Figure 4.--Nonpalinspastic map of distribution of basinal facies (horizontal lines) and bounding subtidal and peritidal facies (brick pattern) in Late Cambrian (middle Franconian time). Localities mentioned in text: N, northern Toiyabe Range; T, southern Toiyabe Range; X, Hot Creek Range; R, Ruby Mountains; H, House Range. Dots show control localities.

During middle Middle Cambrian time (*Ptychagnostus gibbus* Chron) conditions changed abruptly, and basinal rocks of the Wheeler Formation and lithic equivalents were deposited in a broad belt across much of Nevada and Utah (Robinson, 1964; Kepper, 1972, 1976, 1981), initiating the House Range embayment, an eastward extension of deeper water into Utah (fig. 2). The basin, fault-bounded near the Nevada-California line (Kepper, 1981) and perhaps along much of its southeastern boundary, was relatively ephemeral as a topographic low. Although fine-grained gravity-flow deposits locally associated with soft-sediment slumps in the Drum Mountains of Utah (Grannis, personal commun., 1981) attest to initial relief, virtually all of the Utah part of the basin

was infilled by westward prograding sediment by the middle of the succeeding *Ptychagnostus atavus* Chron. Within Utah, deep-water deposits of this age are limited to the southern part of the House Range. In Nevada, although a small, probably silled basin may have persisted throughout the remainder of Middle Cambrian time near the Snake Range, upper Middle Cambrian rocks across most of the east-central part of the state generally shoal upwards. Stromatolites and flat-pebble conglomerates occur in this succession as far west as the Ruby Range. Basinal deposits accumulated throughout the Middle Cambrian only in the most westerly Cambrian exposures in Nevada, in a belt extending southward from the Osgood Mountains through the Toiyabe Range to near Goldfield in Esmeralda County.

Renewed differential subsidence and sedimentation in latest Middle Cambrian time (*Lejopyge calva* Chron) initiated a pattern that persisted throughout the lower two-thirds of the Dresbachian Stage of the Upper Cambrian (fig. 3). Our interpretation of the paleogeography of this interval differs in detail from that of previous authors (Palmer, 1971). We consider that a basinal area separated the main carbonate platform of the southeastern Great Basin from a carbonate shoal to the west. This western shoal is represented today by the subtidal and peritidal carbonate beds of the Hamburg Dolomite of Eureka, the Roberts Mountains, and Cortez. It presumably shed fine-grained carbonate material eastward, but slopes to the east were at a low angle. The coeval laminated, carbonate-rich basinal rocks of the Ruby Range show no indication of soft-sediment movement or debris flow. Their fauna consists only of poorly preserved kormagnostids in the lower beds and sparse *Glyptagnostus* higher in the sequence. The absence of a benthic fauna suggests anoxic bottom conditions, but this may have been a local feature, for polymeroids of the basal *Aphelaspis* Zone are associated with *Glyptagnostus* in the upper part of the basinal Swarbrick Limestone of Mount Hamilton and the Hot Creek Range (Palmer, 1965) still farther to the south.

The Eureka-Roberts Mountains shoal also shed fine carbonate material to the west. In the Callaghan window of the northern Toiyabe Range, unit B<sub>4</sub> is not the equivalent of the Eldorado Dolomite as was previously thought (Stewart and Palmer, 1967), but seemingly is the same age as part of the Hamburg Dolomite. It is underlain by beds carrying an upper Middle Cambrian ptychagnostid fauna, and, higher in the sequence, unit B<sub>6</sub> has yielded *Glyptagnostus* and *Acmarrhachis* associated with sparse, poorly preserved polymeroids. The approximately 700-m-thick carbonate unit, B<sub>4</sub>, consists largely of a monotonous sequence of fine laminated, hemipelagic and gravity-flow deposits locally contorted by soft-sediment slumping, suggesting that slopes on the west of the shoal may have been steeper than those on its eastern flank.

Throughout the remainder of Late Cambrian time, the sedimentation rate, in general, equaled or exceeded the rate of subsidence. The relief apparent during the middle Dresbachian in east-central Nevada was lost as the Ruby Basin filled (compare figs. 3 and 4). Earliest deposits of this phase constitute the Dunderberg Shale and its lithic equivalents. The unit is readily recognizable across much of the Great Basin by its high terrigenous clay content, but it clearly accumulated in widely different depths, as revealed by features of the interbedded carbonate strata. This episode of terrigenous input was followed by carbonate-dominated deposition throughout the rest of the Cambrian except in the area of outcrop of the western basinal facies (fig. 4). During the middle and late Elvinia Chron (early Franconian), carbonate beds formed a gently sloping sublittoral ramp extending westward from near the House Range (Brady and Rowell, 1976). Subsequently, during the late Franconian and Trempealeuan, shallow subtidal and peritidal carbonate deposits of the Notch Peak and Whipple Cave Formations (Taylor and Cook, 1976) prograded irregularly westward over the deeper water ramp facies. Seaward, the coeval upper part of the Windfall Formation, although less well known, may have formed a westerly-directed ramp from this carbonate shoal.

Because the spectacular slump deposits and associated beds in the Hot Creek Range are also of late Franconian and Trempealeuan age (Taylor and Cook, 1976), at least locally the ramp slope either was unstable or a distinct carbonate shelf-slope break was present. Sedimentological and faunal data led Cook and Taylor (1977) to conclude that these rocks, the lower Hales Limestone, formed on the continental slope of western North America, a conclusion that we initially accepted (Rowell and others, 1979), believing that the continental shelf-slope break trended generally northwards. We now have reservations about this conclusion.

There is no question that the Hales Limestone accumulated on a west-facing slope. The point at issue is whether it is the continental slope. Taylor and Cook (1976) estimated water depth in the Hot Creek Range to have been at least 350 m and considered that depths of more than 1000 m were more probable. It is unlikely that this greater depth value persisted to the north. In the northern Toiyabe Range, laminated limestone contains a fauna of the high Elvinia Zone (Stewart and Palmer, 1967). Many of these specimens are complete trilobites, and the fauna is seemingly both autochthonous and of typical North American aspect; these Franconian deposits accumulated above the thermocline. Higher Franconian and Trempealeuan rocks are dark, laminated, calcareous silt-shale and interbedded clay-shale that have yielded only Lotagnostus and a questionable Bienvillia (Stewart and Palmer, 1967). Slump deposits and the deep-water

similar to those of the somewhat older slump deposits in the Hot Creek Range. The Goodwin Limestone in the Callaghan window, however, is part of a shoaling-upward sequence. Its upper beds are strongly bioturbated and were probably deposited in depths of no more than a few tens of meters. Because the Goodwin Limestone of this area is only about 300 m thick, a first-order approximation of maximum water depth for accumulation of the slump deposits at its base is 300 m. The actual value may have been considerably less if subsidence was concomitant with deposition.

In the southern Toiyabe Range, two distinctly different Upper Cambrian successions are juxtaposed by the Eastside thrust fault Stewart and McKee, 1977). The structurally lower succession, represented by the Broad Canyon sequence, is poorly known but consists predominantly of terrigenous clay-shale beds. Contemporaneous, but structurally higher beds, constitute the Crane Canyon sequence (Stewart and McKee, 1977). The magnitude of displacement along the Eastside thrust is unknown, but the Crane Canyon sequence seemingly was deposited some considerable distance to the west of the Broad Canyon sequence, yet its upper beds contain a much higher percentage of carbonate material. Our reconnaissance studies of the Franconian part of the Crane Canyon sequence show that coarse resedimented conglomerates, probably debris-flow or slump deposits, are associated with laminated calcareous silt-shales. We have yet to be able to determine the transport direction of the conglomerates from fabric studies, but regional considerations suggest that the source was probably to the west. This is the evidence for the carbonate shoal tentatively shown west of the Toiyabe Range (fig. 4). If this interpretation is correct, it is apparent that the configuration of the continental margin was more complex than has been previously envisioned. Either the continental slope in the area of the Hot Creek Range had a more tortuous path than previously has been suspected, or alternatively, and we consider more probably, the slump deposits in the Hot Creek Range formed on a slope between a carbonate platform and a deep, outer shelf basin. In the latter interpretation, the westernmost basinal rocks were deposited not in an oceanic site but in a deep, outer marginal basin that was at least partially bounded by yet another carbonate-shoal complex still farther to the west. The continental shelf-slope break would have been west of this shoal, and the only Cambrian rocks in Nevada that were deposited oceanward of the continental shelf are the feldspathic quartzite and chert of the allochthonous Harmony Formation and Paradise Valley Chert (Rowell and others, 1979). Seemingly, the Hedinaspis fauna are presently unknown from the Cambrian of this area. Slump deposits occur, however, in the lower part of the overlying Goodwin Limestone of Early Ordovician age. Coarse conglomerates are

remaining basinal deposits of the Cambrian of Utah and Nevada accumulated in outer shelf basins characterized by differing degrees of temporal persistence. The more easterly ones, closer to shoal water and sediment source, were relatively ephemeral; the westerly basin persisted as a topographic low into the Ordovician.

We are grateful to R. A. Robinson and A. R. Palmer for trilobite identifications, and to Robinson for innumerable discussions of the Cambrian of the Great Basin. We are also indebted to Molly Knudtsen for graciously providing access to her land in the northern Toiyabe Range. The work was supported by National Science Foundation, Earth Science Division Grant EAR 79-19973 and University of Kansas General Research Fund Grant 3435.

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## 55. ARCHAEOCYATHID REEFS OF THE SOUTHERN GREAT BASIN, WESTERN UNITED STATES

By

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A diverse fauna of reef-building archaeocyathids occurs in the Lower Member of the Poleta Formation (lower Cambrian, Nevadella Zone) in eastern California and western Nevada. This unit crops out in an area about 100 km by 100 km that straddles the California-Nevada border between Big Pine, Calif. and Goldfield, Nev. The extent to which these archaeocyathids built laterally-extensive, wave-resistant reefs has not been recognized previously.

The lower Poleta contains four main lithofacies: boundstone, oolite, lime mudstone, and shale. Figure 1B shows the distribution of these lithofacies in 14 measured sections (see fig. 1A for localities). (Figure 1A is also a map showing the relative original positions of each of the 14 sections). The thickness of the limestone that defines the lower Poleta is variable, ranging from 25 m at Waucoba Spring to more than 200 m at Silver Canyon. The vertical sequence of facies also is variable. The Nevada localities normally have oolite overlying boundstone, but at some localities one of these facies is missing. The sequence in the California sections is unpredictable. In general, a single facies in one section cannot be correlated with a single facies in another. The original distribution of the facies was evidently patchy, just as it is in modern reef-shoal settings.

The archaeocyathid systematics of the Poleta Formation has been described by Gangloff (1975, 1976), and other paleontological aspects of this unit are described by Firby and Durham (1974), Nelson (1976), and Rowell (1977). Moore (1976a, b, c) studied the depositional environments of the Poleta Formation and associated units. I have interpreted the depositional environments of the lower member of the Poleta Formation (Rowland, 1978), which contains the most abundant and diverse archaeocyathid fauna in the Great Basin. I have divided the lower Poleta into two facies complexes: an oolite shoal complex and a reef-lagoon complex. In the present paper, I will describe and interpret the archaeocyathid-algal boundstones of the reef-lagoon complex.

### ARCHAEOCYATHID-ALGAL BOUNDSTONES Description

The boundstones of the lower Poleta typically are bold outcrops of blue-gray limestone dappled with conspicuous orange patches of sucrosic dolomite. Varying densities of stick-shaped and dish-shaped

archaeocyathids are in a matrix of dark-gray, millimeter-size speckles of Renalcis and centimeter-size splotches of light-gray lime mud. Renalcis and Epiphyton (both of which were probably algae) are common in thin sections.

The orange dolomite patches, that are diagnostic of the boundstone facies, are typically 50 cm to more than a meter in diameter. They account for about 5 percent of the total volume of the boundstone facies. The boundaries of the dolomite patches with the surrounding boundstone is always sharp, and they are clearly primary features. Many patches contain coarse archaeocyathid debris, and some are finely bedded.

Two distinctive subfacies of the boundstone facies are identifiable at the Stewart's Mill locality. The lower 25 m of the 40-m-thick boundstone facies is dominated by Renalcis. In this Renalcis-dominated subfacies, a variety of archaeocyathids is present, but the archaeocyathids are sparsely distributed and none are branching. The upper 15 m is a different subfacies dominated by dendroid-branching archaeocyathids. Figure 2 is an oblique view of a block of this archaeocyathid-dominated subfacies. This diagram, which was constructed from 5-mm-thick serial slabs, clearly shows the framework fabric of the branching archaeocyathids in the archaeocyathid-dominated subfacies.

The archaeocyathid-dominated boundstones often are intimately associated with oolites. At the Stewart's Mill locality, where facies relationships are unusually clear, three biostromes of the archaeocyathid-dominated boundstone are interbedded with oolite in the upper part of the section. Irregularly shaped, bread-box-size heads of boundstone with densely branching archaeocyathids can be found to project upward and laterally into the overlying oolite. In some places, individual archaeocyathids are rooted in boundstone and surrounded by oolite. It is always the archaeocyathid-dominated subfacies that is found associated with the oolite.

Another facies that sometimes is found associated with the boundstones is a shale that contains lenses of skeletal wackestone (terminology of Dunham, 1962). At the Stewart's Mill locality, some skeletal wackestone beds can be traced stratigraphically upward from the shale into adjacent boundstone masses.

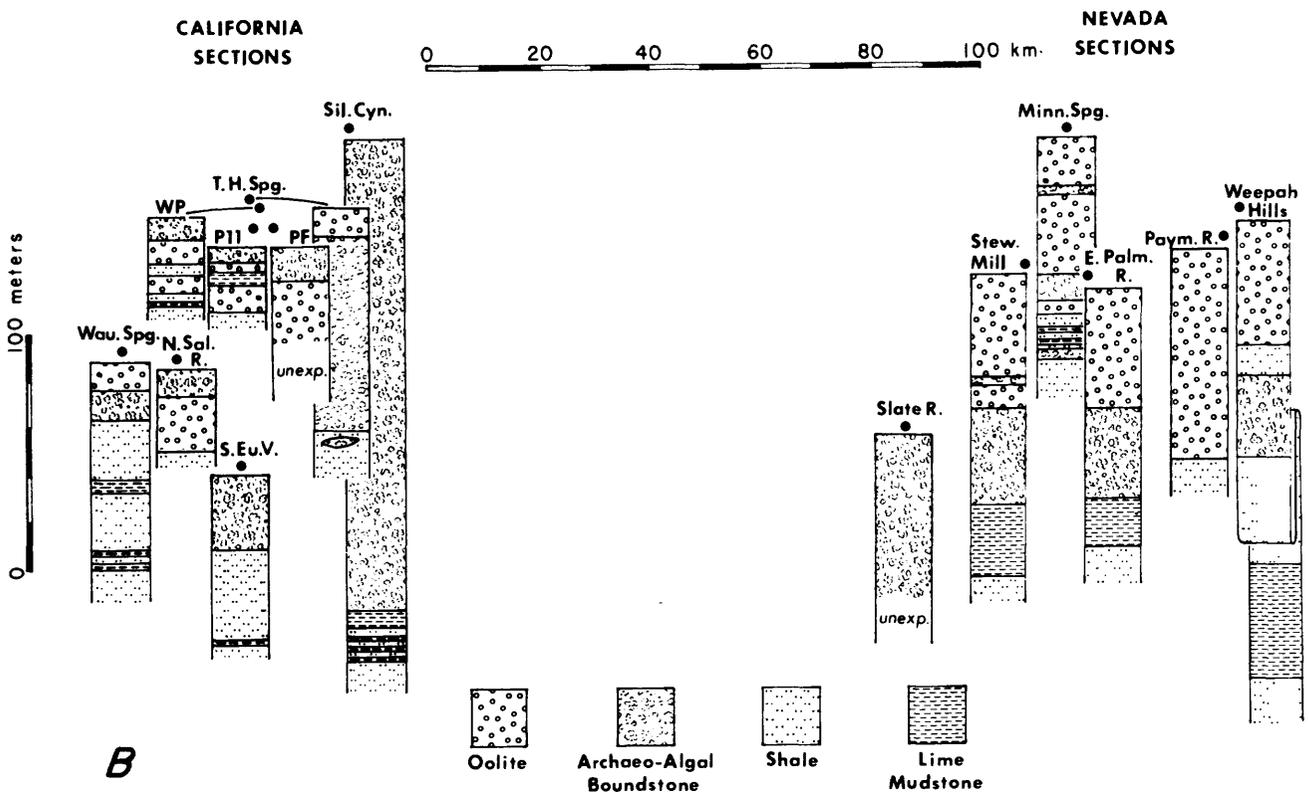
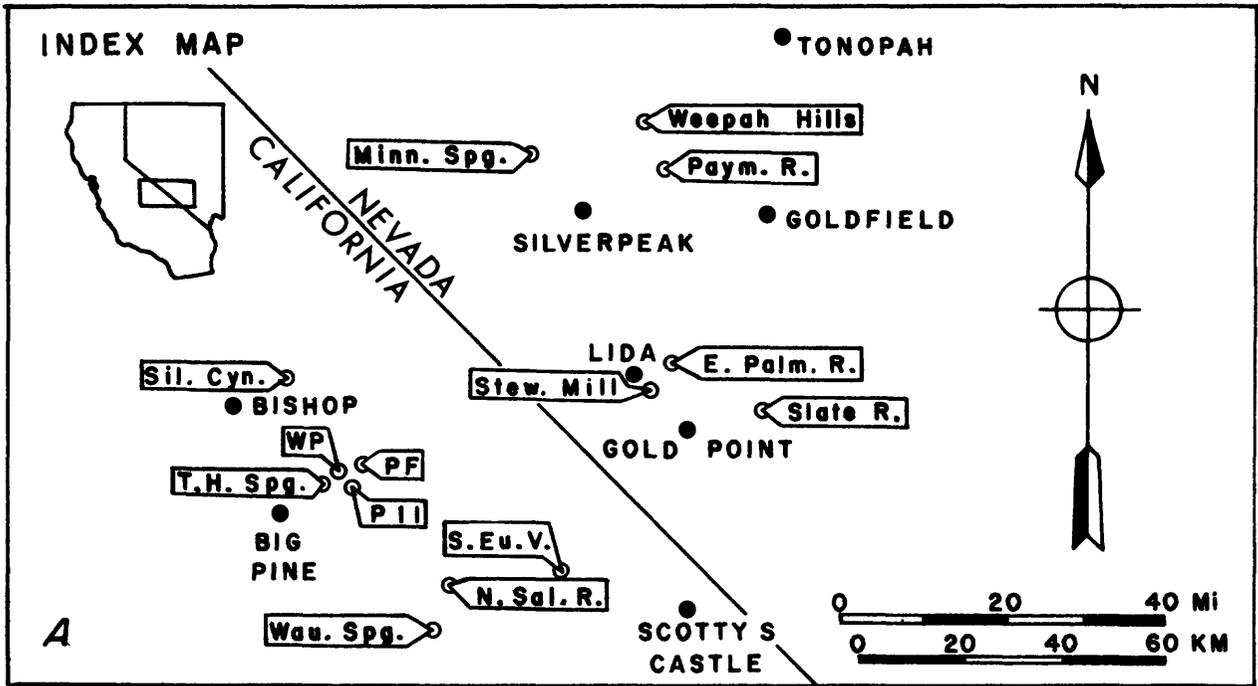


Figure 1.--A, Index map showing localities of 14 generalized measured sections of the lower member of the Poleta Formation and parts of the underlying Campito Formation; B, main lithologies. Campito-Poleta contact generally is placed at base of lowest thick limestone bed. Positions of black dots above sections in B show inferred original relative positions prior to oroflexure and strike-slip faulting along the Death Valley-Furnace Creek Fault Zone as interpreted by Stewart (1967). Some thickness data from Moore (1967a).

## Interpretation

I interpret most of the rocks that contain archaeocyathids to be biologically-bound limestones (boundstones of Dunham, 1962). Skeletal packstones and wackestones are common, but almost always constitute a minor part of the total volume of the archaeocyathid-bearing limestones of the lower Poleta. Previous workers interpreted these rocks differently. Gangloff (1976), for example, in describing the lower Poleta, concluded that "very little boundstone was formed" (p. 27). Moore (1976b) described an archaeocyathid-bearing biohermal limestone as one of five lower Poleta lithofacies, but said that it formed "a minor part of the lower member" (p. 25) and that it, in fact, was "not biologically bound reef limestone" (p. 26).

The reason that the abundance of boundstone in the lower Poleta has not been recognized until now is that unless the rocks are well exposed and well preserved, the arrangement of the fossils is difficult to determine. As seen in Figure 2, the two species that formed dendroid colonies often grew horizontally. At many localities, especially the frequently visited ones in the White-Inyo Mountains, the fossils are indifferently or poorly preserved, and prostrate branches of dendroid colonies appear to be isolated fragments.



Figure 2.--Oblique view of block of archaeocyathid-dominated boundstone from Stewart's Mill locality. Diagram constructed from serial slabs, each about 5 mm thick. Two species are shown, both of which formed complex dendroid colonies. Stippled species is Protopharetra sp., an irregular archaeocyathid. Striped species is an undescribed regular archaeocyathid. Protopharetra species is the most common archaeocyathid in the archaeocyathid-dominated subfacies at Stewart's Mill.

I interpret the meter-size dolomite patches within the boundstone facies to have been tunnels and channels that became choked with lime mud and skeletal debris. These mud-filled channels were later preferentially dolomitized.

The intimate association of oolites with the archaeocyathid-dominated subfacies is strong evidence that this subfacies grew in high-energy conditions. Migrating oolite shoals appear to have, at times, overwhelmed and buried archaeocyathid-algal communities. The interbedded nature of boundstone biostromes with oolites at Stewart's Mill suggest that when oolite shoals became stabilized the archaeocyathid-algal community was able to move in and re-establish itself.

An ecological zonation of the lower Poleta reefs is suggested by the fact that two subfacies of boundstones exist. The archaeocyathid-dominated subfacies consisted of a rigid framework of branching archaeocyathids that could withstand high-energy, ooid-generating conditions. The Renalcis-dominated subfacies did not have a rigid framework, and was, in all probability, restricted to lower energy environments.

The shales with lenses of skeletal debris that locally interfinger with the boundstones are interpreted to represent inter-reef settings where wave-washed reef material accumulated. Modest relief on the order of meters is indicated by the skeletal wackestone lenses that can be traced from reef boundstones into adjacent offreef shales.

## PALEOGEOGRAPHY

The major feature of the Early Cambrian paleogeography of the southern Great Basin were elucidated by Stewart (1970). Figure 3 shows the paleogeography at the time of lower Poleta deposition. Although the outcrop area of the Poleta Formation is a 100 km by 100 km square, after palinspastic restoration of oroflexure folding in western Nevada (Albers, 1967) and right-lateral displacement on the Death Valley-Furnace Creek fault zone (Stewart, 1967) it forms a linear band about 200 km long and 50 km wide. I have placed the lower Poleta reefs and shoals near the shelf margin on Figure 3. Unfortunately the deeper water sediments that should have been directly to the northwest, if preserved at all, are obscured in the metamorphic roof pendants of the Sierra Nevada.

Figure 3 shows that the Poleta sediments accumulated at a latitude of 20°N., with the continent rotated 90° from its present orientation. This orientation is based on paleomagnetic data reported by Cowie (1971) that indicate a Lower Cambrian North American north pole at 158°E., 12°N. and an equator running through Texas and the Dakotas. This position agrees closely with the Late Cambrian position of North America shown by Scotese and others (1979).

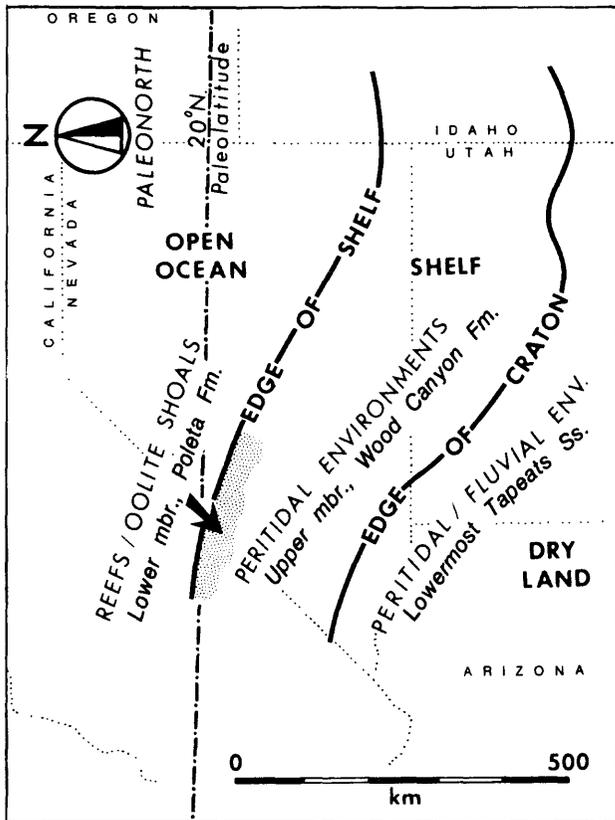


Figure 3.--Paleogeographic setting of the archaeocyathid reefs of the southern Great Basin.

When Figure 3 is viewed with paleonorth at the top, it is easy to imagine that the lower Poleta reefs and shoals were in a favorable position for carbonate production. Northeasterly tradewinds would have driven a westward current parallel to the shelf edge. Warmed by a southward deflection into what is now northeastern Nevada, this westward current would be blown onto the shallow shelf by the northeasterly tradewinds at precisely the location of the lower Poleta reefs and shoals.

#### SUMMARY AND CONCLUSIONS

The lower Poleta boundstones were built by a community of solitary and dendroid-branching archaeocyathids, *Renalcis*, and *Epiphyton*. They are commonly tens of meters thick and volumetrically comprise a major part of the lower Poleta. They formed wave-resistant, cavernous, ecologically zoned, reefs of modest relief. Unlike the archaeocyathid bioherms of Siberia (Zhuravleva, 1972) and Labrador (James and Kobluk, 1978) the lower Poleta reefs are not discrete, outcrop-size lens or mound-shaped bodies. Rather, they are laterally continuous for at least hundreds of meters. They formed in a complex, 50-km-wide, shelf-margin mosaic of reefs, oolite shoals, islands, and lagoons at a latitude of approximately 20°N.

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## 56. BIOSTRATIGRAPHY OF CAMBRIAN MOLLUSKS

By

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Until recently, little attention was paid to Cambrian mollusks partly because they are far less common than post-Cambrian mollusks but also because many are microfossils and are therefore much smaller than their post-Cambrian counterparts. The simultaneous development, in the last 15 years, of scanning electron microscopy, international interest in the Precambrian-Cambrian boundary, and a model for the early radiation of the phylum (Runnegar and Pojeta, 1974) has resulted in a large amount of new research on these organisms. It is now becoming clear that not only do Cambrian mollusks provide the key to an understanding of the early history of the phylum, they also have potential for dating and interpreting Cambrian rocks.

A clear knowledge of the taxonomy of Cambrian mollusks is needed before other studies can proceed much further. About 150 generic names and more than 450 specific names have been given to Cambrian mollusks in the last hundred years, but about half of these are synonyms, and the stratigraphic and biogeographic ranges of the 'real' genera and species are poorly known. The taxonomy has been complicated by the preservation of many Cambrian mollusks as phosphatic internal molds and the inexperience of many authors who were or are accustomed to other phyla and other modes of preservation.

Since about a half of the described genera and about a third of the described species are from the Cambrian of China, it has been important to concentrate on this area first. Other important regional sources of taxa are Australia, North America, northern Europe and Siberia.

In order to examine the biostratigraphy and biogeography of Cambrian mollusks, five regions have been selected for study: China-Korea, Australia-New Zealand, North America, Europe-Avalonia, and Siberia. The first three regions provide useful data from the whole of the Cambrian, the fourth for the Early and early Middle Cambrian, and the last for the Early Cambrian only. Ranges of genera and species plotted against local time-divisions from each region have been compared by constructing a correlation chart for the five areas. Since good mollusk faunas occur on a limited number of horizons in each region, a global compilation is needed to provide any realistic picture of generic ranges.

### IMPORTANT FAUNAS FROM THE FIVE REGIONS China-Korea

Mollusks are scattered through the Middle and Late Cambrian limestone of north China and Korea, but most of the taxa so far described are either of earliest (Meishucun) or latest Cambrian (Fengshan) age. The former are from the southern provinces of Hubei (Hupeh), Sichuan (Szechwan), and Yunnan, while the latter are best known from the northern provinces of Liaoning, Shandong (Shantung) and Anhui (Anhui).

The Meishucun mollusks occur in thin phosphatic beds which lie disconformably upon the thick Dengying (Tengying, Tŕngying) Dolomite of late Proterozoic age. They are succeeded by strata containing very old Early Cambrian trilobites and are thought to be possibly 'pre-trilobite' and equivalent to the Tommotian of Siberia (Chang, 1980). The mollusks are preserved as small or microscopic phosphatic internal molds.

At least 44 new generic names and 71 new specific names were proposed for Meishucun microfossils identified as mollusks between 1974 and 1980 (Yŕ, 1974, 1979; Lu, 1979; Jiang, 1980; Chen and Zhang, 1980; He, 1980). A careful examination of the literature, type specimens stored in Nanjing, and comparative material collected from the Yangtze Gorge section in Hubei has demonstrated that much of the taxonomy is unrealistic and impractical. Many of the taxa result from preservational artifacts, some are not mollusks, and there are unappreciated similarities with the Tommotian faunas of Siberia and with the undescribed fauna of the Parara Limestone of South Australia. Despite this, the Meishucun faunas are most important: they are very old, very diverse, and have yielded taxa such as the macluritacean gastropod Cambrospira Yŕ, the rostroconch Heraultipegma Pojeta and Runnegar, and a variety of scenellids and helcionellids.

The Fengshan mollusks are found in the 20-30 m thick stromatolitic Wanwangou (Wanwankou) Limestone in Liaoning, and in its equivalents in the Fengshan Formation in Shandong and Anhui. By contrast with the Meishucun faunas, the Fengshan mollusks are large and are principally gastropods, rostroconch and cephalopods (Kobayashi, 1933; Pojeta and Runnegar, 1976; Chen and others, 1979a, b).

Previously considered to be Ordovician, these faunas are now regarded as latest Cambrian by Chinese geologists because they occur below Cordylodus proavus and Staurogriaptus diffisus, contain what are thought to be latest Cambrian trilobites (Zhou Zhi-yi, personal communication), and have different cephalopods from the earliest Ordovician of the United States. They must, however, be very close to the Cambrian-Ordovician boundary.

#### Australia-New Zealand

All significant Australian occurrences of Cambrian mollusks so far discovered lie in a central zone extending from the Adelaide region, through eastern South Australia, western New South Wales, the southern part of the Northern Territory to north-western Queensland. The best described faunas are from the Middle Cambrian (Runnegar and Jell, 1976, 1980) and the late Late Cambrian (Pojeta, and others, 1977), but undescribed well-preserved assemblages occur in the Early Cambrian of South Australia and the early Late Cambrian (Mindyallan) of Queensland and the Northern Territory.

A diverse and largely undescribed fauna of phosphatic micromollusks occurs in the Parara and Ajax Limestones of South Australia (Daily, 1956). Archaeocyaths from these units are most similar to those of the Atdabanian and early Lenian of Siberia (Kruse and West, 1980; D. Gravestock, personal communication), while some of the trilobites from the Parara Limestone resemble Parabadiella and Proichangia of the post-Meishucun Chiungchussu Stage in China (P.A. Jell, personal communication). The Parara fauna, which includes the bivalve Pojetaia Jell, a new macluritacean gastropod, Pelagiella subangulata (Tate), Obtusocoelus Yb, Stenothecca Hicks, Anabarella Vostokova, Bemella Missarzhevsky, and a number of other taxa, is probably just a little younger than the Meishucun and Tommotian.

Undescribed faunas dominated by Scenella reticulata Billings occur in younger units in southern Australia, but are not yet well researched. A diverse latest Early Cambrian or earliest Middle Cambrian assemblage from the First Discovery Limestone in western New South Wales (Runnegar and Jell, 1976, 1980) contains representatives of such distinctive genera as Yochelcionella Runnegar and Pojeta and Protowenella Runnegar and Jell, as well as rugose species of Latouchella Cobbold. Similar taxa are also found in the Floran Currant Bush Limestone of the early Middle Cambrian of Queensland (Runnegar and Jell, 1976), but few mollusks have been recovered from the later Middle Cambrian.

This interval may be covered by an undescribed fauna from the ?late Middle Cambrian Tasman Formation of New Zealand (MacKinnon, 1980). This

assemblage contains genera such as Pelagiella Matthew, Protowenella, and Mellopegma Runnegar and Jell, as well as a new genus allied to Eotebenna Runnegar & Jell and the only known Middle Cambrian bivalve (MacKinnon, in preparation).

The Australian Late Cambrian mollusk faunas are dominated by rostroconchs (Pojeta and others, 1977) and gastropods (Opik, 1967). The latter have not been described, but the oldest known occurrences of Matherella Walcott and Clisospira Billings are from the Mindyallan of central Australia (Runnegar, in press).

#### North America

As in China and Australia, mollusks are scattered through the Cambrian strata of the United States and Canada, but few diverse faunas have been described so far. Those of significance are from the Early Cambrian of New York and Quebec and the Late Cambrian of Wisconsin, Missouri, and New York.

The latter are dominated by large gastropods and monoplacophorans such as Scaevogyra Whitfield, Hypseloconus Berkey, 'Ozarkoconus' Heller, and Proplina Kobayashi, although the chiton Matthevia is also widespread (Runnegar and others, 1979). The former are known from the Taconic sequences in New York (Lochman, 1956) and fossiliferous boulders of the Ordovician conglomerates of Quebec; they include the bivalve Fordilla troyensis Barrande (Pojeta, 1975), Pelagiella atlantoides (Matthew), P. primaeva (Billings), and Helcionella subrugosa (D'Orbigny).

#### Europe-Avalonia

Small molluskan faunas are known from isolated Early and early Middle Cambrian localities in Denmark (Poulsen, 1967; Berg-Madsen and Peel, 1978), southern France (Cobbold, 1935), Czechoslovakia (Horny, 1964), Wales, Newfoundland (Walcott, 1891) and Massachusetts (Shaler and Foerste, 1888), and the Early Cambrian gastropod Aldanella Vostokova has been recovered from a number of sites in Poland, Estonia, and Norway (Posti, 1978; Flyn and Glaessner, 1979).

The North American occurrences are of late Callavia zone age. The best localities are in the Brigus Formation of southeast Newfoundland, which has yielded Fordilla troyensis Barrande, Aldanella attleboroensis (Shaler and Foerste), Scenella reticulata, Stenothecca acutacosta Walcott, Pelagiella primaeva, Igorella terranovica (Resser) and Yochelcionella erecta (Walcott). This occurrence confirms the Early-Middle Cambrian range for Yochelcionella suggested by Runnegar and Pojeta (1980), since it occurs with Serrodiscus bellimarginatus and Meniscuchus helena.

## Siberia

Important faunas of Tommotian mollusks are well described from a number of sections in Siberia (Vostokova, 1962; Rozanov and Missarzhevsky, 1966; Rozanov and others, 1969; Missarzhevsky, 1974; Matthews and Missarzhevsky, 1975). They have Aldanella and Heraultipegma in common with Early Cambrian faunas of Europe and Avalonia, and Purella Missarzhevsky, Bemella, and possibly species of Latouchella in common with the Meishucun assemblages of China. Younger beds in Siberia have yielded Fordilla sibirica Krasilova, the distinctive genus Tannuella Missarzhevsky, and Pelaqiella, all of which are of Atdabanian age.

## CONCLUSIONS

1. Common, distinctive, and widespread genera have relatively long stratigraphic ranges; those with short ranges are generally known from few localities.

2. Phosphatic internal molds are useful and identifiable but provide less information than preserved shells, silica replicas or conventional casts and molds. They should therefore be used cautiously when new taxa are proposed.

3. Individuals from a single sample can vary greatly in size and shape. Large populations are required for good taxonomy unless the forms are distinct and new.

4. Despite the fact that at least four major classes of the Mollusca (Monoplacophora, Gastropoda, Bivalvia, and Rostroconchia) had evolved by the end of the Tommotian, generic and specific diversity remained low and relatively constant until the later part of the Late Cambrian. By the end of the Cambrian the phylum was diversifying at a more-than-exponential rate, with the result that mollusks became a major component of the shelly faunas of the Ordovician and younger periods.

5. The Cephalopoda did not evolve until the latest Cambrian, and the best record of this event is to be seen in the platform carbonates of north China.

6. Discoveries of new Cambrian mollusks, which have been made at a greatly accelerating rate in the last seven years, are helping to confirm Runnegar and Pojeta's (1974) model for the early evolution of the phylum and are tending to disprove other theories.

7. The maximum size of mollusks increased throughout the Cambrian.

8. The best place to look for phosphatised Cambrian micromollusks is on disconformity surfaces in epicontinental carbonate sequences.

9. By the Late Cambrian, a variety of mollusks had invaded the stromatolitic littoral zone of clastic shorelines and offshore carbonate banks. This may not have been true in earlier times.

10. Genera and species of Cambrian mollusks are surprisingly widespread when it is considered that they probably inhabited very proximal environments. For example, Yochelcionella has now been found in Australia, North America, and Greenland; Scenella reticulata occurs in South Australia and Newfoundland; Fordilla bridges the 'Protoatlantic'; Scaevogyra, Proplina, and 'Ozarkoconus' lived synchronously near shorelines in Liaoning and Wisconsin. The ecology and biogeography of Cambrian mollusks are subjects worthy of further research.

11. Mollusks can be used now to date Cambrian rocks, but the resolution should improve greatly in the next ten years.

Acknowledgements.--This study was supported by the Australian Research Grants Committee (grant no. E7915353), the Australian Academy of Science, Academia Sinica, and the University of New England. I thank Chris Bentley, Peter Jell, John Pojeta, Jr., David MacKinnon, Xu Jun-tao, Yü Wen, and Zhang Wen-tang for all sorts of help.

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## 57. THE UNIQUENESS OF THE CAMBRIAN FAUNA

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The fauna of every period of geologic time is unique to a certain extent. New species constantly evolve and old species continually become extinct; habitats change as do configurations of biogeographic provinces. Such dynamics keep faunas continuously changing. There are, however, certain major pivotal points in the history of marine faunas when this change is greatly accelerated. Two such pivotal points, the Vendian-Cambrian evolutionary radiations and the Ordovician evolutionary radiations, bound the Cambrian Period with the results that its fauna appear more distinctive than most. In this essay I shall briefly review three aspects of the Cambrian fauna, its diversity, taxonomic composition, and ecological organization, and attempt to show that the Cambrian fauna appears truly unique when viewed against the whole of the Phanerozoic Eon.

### DIVERSITY

Discussions of diversity in the Cambrian traditionally have focused upon the problem of the Precambrian-Cambrian boundary, which at times has been described as the greatest discontinuity in the history of life. Increased knowledge of the nature and sequence of late Precambrian and Early Cambrian fossils has shown, however, that the Precambrian-Cambrian boundary represents more of a rapid transition than a distinct discontinuity (Zhuravleva, 1970; Stanley, 1976). I have argued elsewhere (Sepkoski, 1978, 1979) that the "explosion" in diversity apparent in the Early Cambrian represents nothing more than what should be expected for the evolutionary filling of an ecologically empty environment: diversity must start low and increase multiplicatively, resulting in a long "lag phase" and a short "exponential growth phase." Current data on number of fossil taxa across the Precambrian-Cambrian boundary do indeed indicate an exponential phase of diversification.

What is perhaps more surprising about Cambrian diversification is that it is slowed down so soon after the start of the period. As illustrated in figure 1, the exponential growth phase of familial diversification lasted only for the first 30 m.y. of the Cambrian; the

next 40 m.y., covering the Middle and Late Cambrian, saw only minor increase in standing diversity. This makes the Cambrian Period appear uniquely depauperate when compared to the rest of the Phanerozoic.

Figure 1 shows that the early phase of growth and later phase of "stagnation" during the Cambrian combine to form one of three distinct intervals in the history of diversification in the oceans. The second, post-Cambrian Paleozoic interval begins with the great Ordovician radiations, which tripled familial diversity in the span of about 60 m.y.; these radiations end in a long phase of nearly constant diversity punctuated only by several moderate extinction events. The final interval of diversification is initiated by the Late Permian extinctions, which reduce familial diversity almost back to Cambrian levels; after these extinctions, diversity increases almost continuously to an apparent maximum in the present oceans.

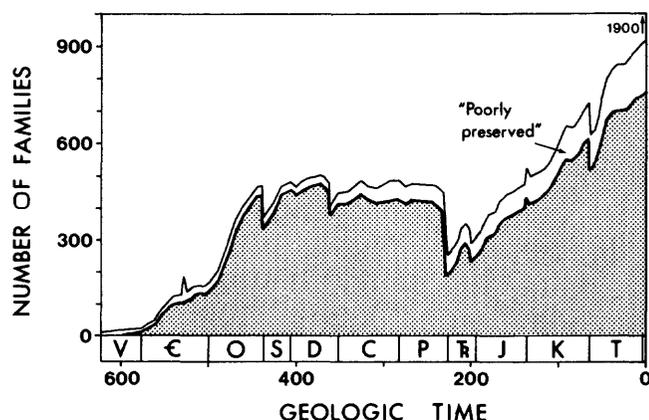


Figure 1.--The Phanerozoic history of diversity of marine animal families. The total standing number of families described from the marine fossil record in each of 81 stratigraphic stages is indicated by the upper curve in the graph. The lower curve, bounding the stippled field, represents the familial diversity of "shelly" animals that constitute the bulk of the fossil record. The unshaded field between the two curves indicates the

known diversity of soft-bodied and lightly skeletonized animals, such as are abundant in the Burgess Shale. About 1900 animal families, most of which are not readily fossilizable, have been described from the modern oceans, as indicated in the upper right of the graph. Note that archaeocyathids, which may not properly belong in the Animal Kingdom (Zhuravleva and Miagkova, 1972; Opik, 1975; Nitecki and Debrenne, 1979), have not been included in this graph; their inclusion would introduce a peak in the diversity curve just to the left of the sharp Cambrian peak in "poorly preserved" families produced by the Burgess Shale fauna.

The data for this figure were derived primarily from the Treatise on Invertebrate Paleontology (Moore and others, 1967), The Fossil Record (Harland and others, 1967), and Vertebrate Paleontology (Romer, 1966). About 300 additional literature sources were used to update and refine this taxonomic and stratigraphic information, particularly as pertaining to the Cambrian Period (see Sepkoski 1979, Appendix I).

#### TAXONOMIC COMPOSITION

A total of about 450 animal families are recognized by contemporary systematists as having occurrences in the Cambrian System. This quantity represents 15 percent of all marine animal families described from the Phanerozoic fossil record. Of the Cambrian families, about 100 belong to the enigmatic Archaeocyatha, which is confined to the Lower and lower Middle Cambrian. Another 75 families represent soft-bodied and lightly skeletonized animals, including many arthropods and problematical taxa which are seen nowhere else in the fossil record. Most of the remaining families of "shelly" animals belong to classes that can be considered as more typical of the Cambrian than of later periods of earth history: 40 percent of the shelly families are trilobites, and another 15 percent are distributed among monoplacophorans, hyolithids, inarticulate brachiopods, and eocrinoids; and about 12 percent belong to minor groups including stenotheccoids, cribricyathids, volborthellids, sabelliditids, several echinoderms classes, and various problematica. Many of these minor groups are confined entirely to the Lower Cambrian. The more important groups, on the other hand, mostly appear very early in the Cambrian and remain diverse throughout that period, giving it a certain faunal continuity through time.

Perhaps the most striking aspect of the assemblage of important Cambrian shelly taxa is that none participate as important elements of the great Ordovician radiations. These radiations, which actually begin just before the close of the Cambrian Period, largely involve groups that appear as insignificant classes during the Cambrian. These include, most notably, articulate brachiopods, ostracodes, gastropods, cephalopods, bivalves, crinoids, anthozoans, graptolites, and conodonts, all of which occur in the Cambrian but together contribute fewer than 15 percent of the families known from that period. The dominant Cambrian groups, on the other hand, contribute less than 25 percent of the total diversity of the Ordovician, and all contain fewer families at the end of the Ordovician than they had at the close of the Cambrian.

This pattern of expansion of new groups and contraction of typical Cambrian groups effects the largest turnover in composition of marine faunas seen in the history of the oceans. To illustrate the rapidity and magnitude of this turnover, I have assembled all classes of marine animals into three major "evolutionary faunas": a Cambrian fauna, a post-Cambrian Paleozoic fauna, and a Mesozoic-Cenozoic, or "modern," fauna (fig. 2). This tripartite division of Phanerozoic families is based on the observation that each of the three intervals of Phanerozoic diversification is characterized by a distinct set of classes that remain important throughout all or most of the interval but are far less important before or after. For example, as noted above, trilobites, inarticulates, monoplacophorans, are important contributors to diversity throughout the post-Cambrian Paleozoic interval but not before or after. The tripartite division of classes is also supported by a multivariate statistical analysis of data on numbers of marine families within metazoan classes through the Phanerozoic (Sepkoski, 1981). This analysis indicates that more than 90 percent of these data can be encompassed by only three factors (that is, uncorrelated linear combinations of classes that tend to vary together in diversity through time); these statistical factors correspond closely to the three evolutionary faunas delimited in figure 2.

As figure 2 illustrates, the transition from dominance by classes constituting the Cambrian evolutionary fauna to dominance by classes of the later Paleozoic fauna is essentially completed by the end of the Ordovician Period; remaining shelly elements of the Cambrian fauna decay slowly in importance thereafter, with only a few inarticulate brachiopods and monoplacophorans surviving until today. In contrast, the transition in dominance from the Paleozoic fauna to the modern fauna is much more slow and gradual; only the turnover associated with the Late Permian extinction exceeds the turnover rate

during the Ordovician Period, and the magnitude of the Permian turnover is much smaller on a proportional basis. The transition from the Paleozoic evolutionary fauna to the modern fauna appear not yet to be completed, so that the total fauna of the present oceans is less dissimilar from the total fauna of the mid-Paleozoic oceans than was the fauna of that particular time from the fauna of the Middle Cambrian oceans, a mere 150 m.y. earlier.

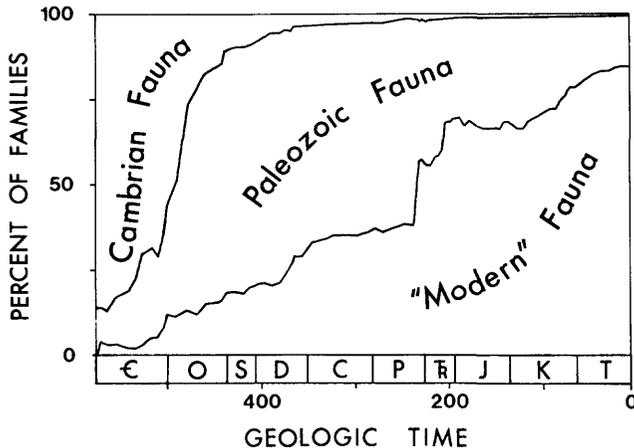


Figure 2.--Changes in the taxonomic composition of marine shelly faunas through time. The three "evolutionary faunas" delineated in this graph represent sets of animal classes that tend to diversify and decline in concert (see text). The principal classes included in each fauna are listed below in order of decreasing diversity:

Cambrian Fauna: Trilobita, Inarticulata, Hyolitha, Monoplacophora, Eocrinoidea, and Pogonophora;

Paleozoic Fauna: Articulata, Crinoidea, marine Ostracoda, Anthozoa, Cephalopoda, Stenolaemata, Polychaeta, Stellerioidea, Graptolithina, Stromatoporoidea, Cystoidea, marine Placodermi, Merostomata, Calcarea, Conodontophora, Blastoidea, Agnatha, Rostroconchia, Tentaculida, Edrioasteroidea, and Stylophora;

"Modern" (or Mesozoic-Cenozoic) Fauna: marine Osteichthyes, marine Gastropoda, marine Bivalvia, Rhizopodea, Gymnolaemata, marine Malacostraca, Echinoidea, Chondrichthyes, Demospongia,

Hexactinellida, Radiolaria, marine Mammalia, marine Reptilia, Amphineura, Cirripeda, and Holothuroidea.

The vertical axis of the graph indicates the proportion of families of "shelly" animals in each evolutionary fauna in each stage of the Phanerozoic.

## ECOLOGICAL ORGANIZATION

Paralleling the change in faunal composition after the Cambrian Period was a major change in the ecological nature of benthic communities. Cambrian communities seem much less structured and well defined than do succeeding Paleozoic communities (Valentine, 1973). As might be expected, within-community diversity is generally low in the Cambrian (Bambach, 1977) as is also between-community diversity. Cambrian organisms are clearly differentiated into biofacies (for example, Jago, 1973; Palmer and Campbell, 1976; Sprinkle, 1976), but this differentiation seems to occur at fairly low taxonomic levels, and often Cambrian communities appear to be broadly intergrading (see further, Palmer 1969; Taylor, 1977). This contrasts to the more tightly defined communities of the later Paleozoic, which often can be easily differentiated at the ordinal and class levels (see further, McKerrow 1978). Within- and between-community habitat and trophic diversities also appear low in the Cambrian. The shelly fauna in most shelf environments apparently was dominated by vagrant deposit feeders (trilobite), whereas high suspension feeders and deep burrowers were rare (Ausich and Bottjer, 1980; Sepkoski and Bambach, 1979). In contrast, the benthic communities established during the Ordovician radiations were dominated by complexly structured assemblages of attached epifaunal suspension feeders.

Just as the taxonomic changes associated with the Ordovician radiations seem to have involved large-scale displacement of one set of taxa by another, the ecological changes seem to have involved displacement of one type of community by another. This displacement appears to have been environmentally controlled, progressing from nearshore to offshore through the Ordovician, as schematically illustrated in figure 3 (see also Berry, 1974). In North America, the first indications of the Ordovician radiations are seen in the uppermost Cambrian (Trempealeuan Stage) with the expansion of molluscs (gastropods, rostroconchs, and probable chitons) in very shallow-water stromatolitic facies (for example, Taylor and Halley, 1974). These groups are joined by articulate brachiopods and cephalopods in similar Lower Ordovician facies, in which trilobites are greatly diminished. Articulate brachiopods and gastropods

also occur in Lower Ordovician mid-shelf facies but are mixed with diverse trilobites and inarticulates; these latter two groups remain solely dominant in contemporaneous outer-shelf and slope facies. In the Upper Ordovician, typical Paleozoic shelly taxa, including articulate brachiopods, bryozoans, and palmatozoans, dominate communities in virtually all shelf facies. Slope facies, however, still retain a peculiarly Cambrian aspect, with ptychoparioid trilobites and inarticulate brachiopods common among the shelly benthos. Even in the Silurian and Devonian, trilobites and inarticulates appear most diverse in deeper water facies (McKerrow, 1978).

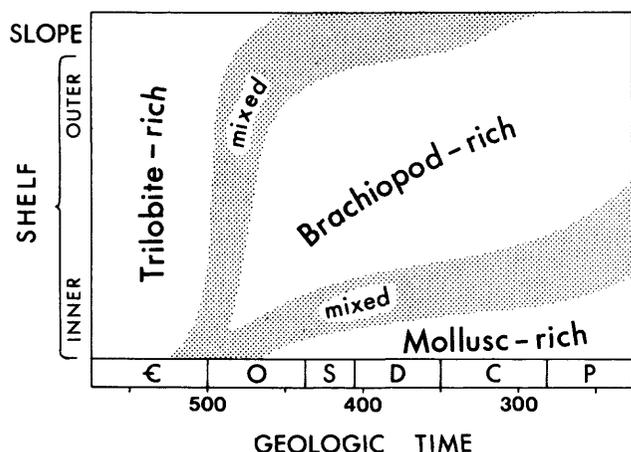


Figure 3.--Diagram showing the general environmental distribution through the Paleozoic Era of Cambrian-type trilobite rich communities, later Paleozoic-type brachiopod-rich communities, and modern-type mollusk-rich communities. The dominant taxa in each group of communities are similar to those in the three evolutionary faunas listed in figure 2. The stippled fields labelled "mixed" schematically delineate times and environments with communities dominated by mixtures of taxa from different evolutionary faunas, as, for example, the mixed trilobite-brachiopod communities of the Early Ordovician shelf and mid-Paleozoic slope. Data for the figure were derived from Berry (1974), Bretsky (1969), McKerrow (1978), and Sepkoski and Sheehan (unpubl.).

The displacement of older style communities into offshore environments is not without parallel in the fossil record. As illustrated in figure 3, molluscan communities with a vaguely modern aspect first appear in Upper Ordovician shallow-water terrigenous facies. These bivalve- and gastropod-rich communities

then expand through the remainder of the Paleozoic (Bretsky, 1969), picking up malacostracans and bony fishes in the Devonian. By the Permian, mixed brachiopod-bivalve communities appear in mid-shelf facies where mixed brachiopod-trilobite communities appeared in the Early Ordovician.

## CONCLUSIONS

The fauna of the Cambrian Period appears unique when compared to faunas across the whole of the Phanerozoic. Only the differences in diversity, composition, and ecology seen between the faunas of the Paleozoic Era and of the combined Mesozoic and Cenozoic Eras rival the differences between the faunas of the Cambrian and of the later Paleozoic. Much of the uniqueness of the Cambrian fauna undoubtedly arises from its unique position in history: it is the Earth's first diverse fauna, and as such represents the completion of the transit from an autotroph- to a heterotroph-dominated world ocean. Many aspects of the Cambrian fauna seem simple or generalized, but the fauna does seem to have an evolutionary coherency so that it survives in essence beyond the bounds of the Cambrian Period as it is being displaced by the more complex fauna of the later Paleozoic.

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## 58. TOWARDS A GLOBAL LATE CAMBRIAN AGNOSTID BIOCHRONOLOGY

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Agnostina Salter, 1864 (agnostids) are small, blind, isopygous arthropods with two thoracic segments, and a simple intratragmatic articulation that permitted sphaeroidal enrollment (in the sense of Bergström, 1973). Traditionally, they have been classified among the Class Trilobita Walch, 1771, but recent discoveries of appendages and visceral morphology (K. J. Müller, oral. commun., Dec. 1980) support other morphological features in suggesting that classification should be sought elsewhere. Agnostina ranged from late Early Cambrian (Protolenus Zone) to Late Ordovician (Ashgillian), and were particularly common during the Middle and Late Cambrian. Nine of ten family groups recognised by Opik (1967, p. 73, table 6) existed during the latter epoch.

Although Agnostina are found in most sedimentary environments, they are most common in and around carbonate bank mosaics, and in contemporaneous outer detrital environments. Agnostid communities replace each other in time more rapidly in carbonate bank environments than in inner or outer detrital ones, but their geographic distribution appears to be more limited as they pass laterally from outer to inner shelf environments. Accordingly, those agnostids living on the outer, ocean-facing margins of carbonate bank complexes and preserved in dark carbonate and shale sequences, seem to have the greatest potential for establishing agnostid-based biostratigraphic schemes. In such environments, there is a general higher organic productivity where warm epicontinental and cooler oceanic waters mingle; sedimentation is more uniform and there is a greater continuity in the organic fossil record; and often there is a mingling of autochthonous and allochthonous faunal elements, the latter having been flushed oceanward from carbonate bank environments, which permits correlation of outer detrital and carbonate belt sediments.

The biochronological potential of Middle Cambrian agnostids has been successfully exploited by Westergård (1946), Robison (1964) and Opik (1961b, 1979). A relatively high degree of resolution has been obtained using Ptychagnostinae and Peronopsidae in the dating of predominantly anoxic Middle Cambrian sediments deposited prior to the Paradoxides forchhammeri Stage of the Baltic and Avalon

Platforms, and its correlatives elsewhere. The full biochronological potential of Late Cambrian agnostids has not been widely recognized to date, although they have been found on and adjacent to all contemporaneous Late Cambrian cratons. Some 64 genera, including eighteen proven or probable synonyms, and several hundred species have been named. Outstanding problems that restrict biochronological analysis of these Late Cambrian agnostids are conceptual, palaeobiological and ecological.

Before 1960, and in some instances subsequently, these agnostids were poorly treated in regional faunal monographs. "Shotgun" determinations, ad hoc systematics often based on a single tagma, small collections, or inadequately preserved and (or) prepared material, have led to the clouding of original taxonomic concepts, and in some cases created dubious biostratigraphy. For the determination of an agnostid taxon, it is currently considered necessary to use as large a paradigm as possible so that maximum morphological variation can be demonstrated, and it is advantageous to have both exoskeletal and parietal surfaces of cephalon and pygidia. For biochronological precision, agnostid assemblages should be derived from detailed measured lithological sequences through which evolutionary lineages can be established, or in their absence, from detailed spot-locality collecting. It is particularly necessary to assess degree of effacement within a given assemblage because in many lineages there is a gradation from en grande tenue to effaced exoskeleton morphology. The end members of such gradations often have received different names.

Although some advance has been made with the clarification of taxonomic concepts and classification of Clavagnostidae (see Opik, 1967; Jago and Daily, 1974) and some Diplagnostidae, particularly Ammagnostinae (see Opik, 1967) and Pseudagnostinae (Shergold, 1977, 1980, and in press), considerable effort is yet required to sort out the concepts of many taxa assigned to Agnostidae. Of these, Glyptagnostinae have particular value in any wide-ranging biochronological scheme (see Kobayashi, 1949; Palmer, 1962; Opik, 1961a, 1963; Shergold, in press). However, although this subfamily is well diagnosed and discrete, its origin (diplagnostid or agnostid) remains

MIDDLE CAMBRIAN	ORDO.	Cordylodus proevus	DATSONIAN
UPPER CAMBRIAN	ORDO.	Microsaukia perplexa	PAYNTONIAN
		Neognostus quasiblobus / Tsinania nomas	PAYNTONIAN
		Sinosaukia impages	
		Rh. clarki maximus / Rh. papilio	pre-PAYNTONIAN
		Rh. biflex / N. denticulatus	
		Rh. clarki prolatus / C. seclatrix	
		Rh. clarki parvulus / C. squamosa	post-IDAMBEAN/pre-PAYNTONIAN
		H. lihenensis	
		Pechashania tercia / P. quarta	post-IDAMBEAN/pre-PAYNTONIAN
		Perchashania secunda / Prochueningia glabella	
		Westusia lata / Rhaetagnostus apsis	post-IDAMBEAN/pre-PAYNTONIAN
		post-Ivingella	
		Ivingella tropica	IDAMBEAN
		Stigmatoa diploma	
		Erixanium sentum	IDAMBEAN
Proceratopyge cryptica			
Glyptagnostus reticulatus	MINDYALLAN		
Glyptagnostus stolidotus			
Acmahachis quasivespa	MINDYALLAN		
Erediaspis eretes			
Zone of passage	MINDYALLAN		
Leopyge laevigata			

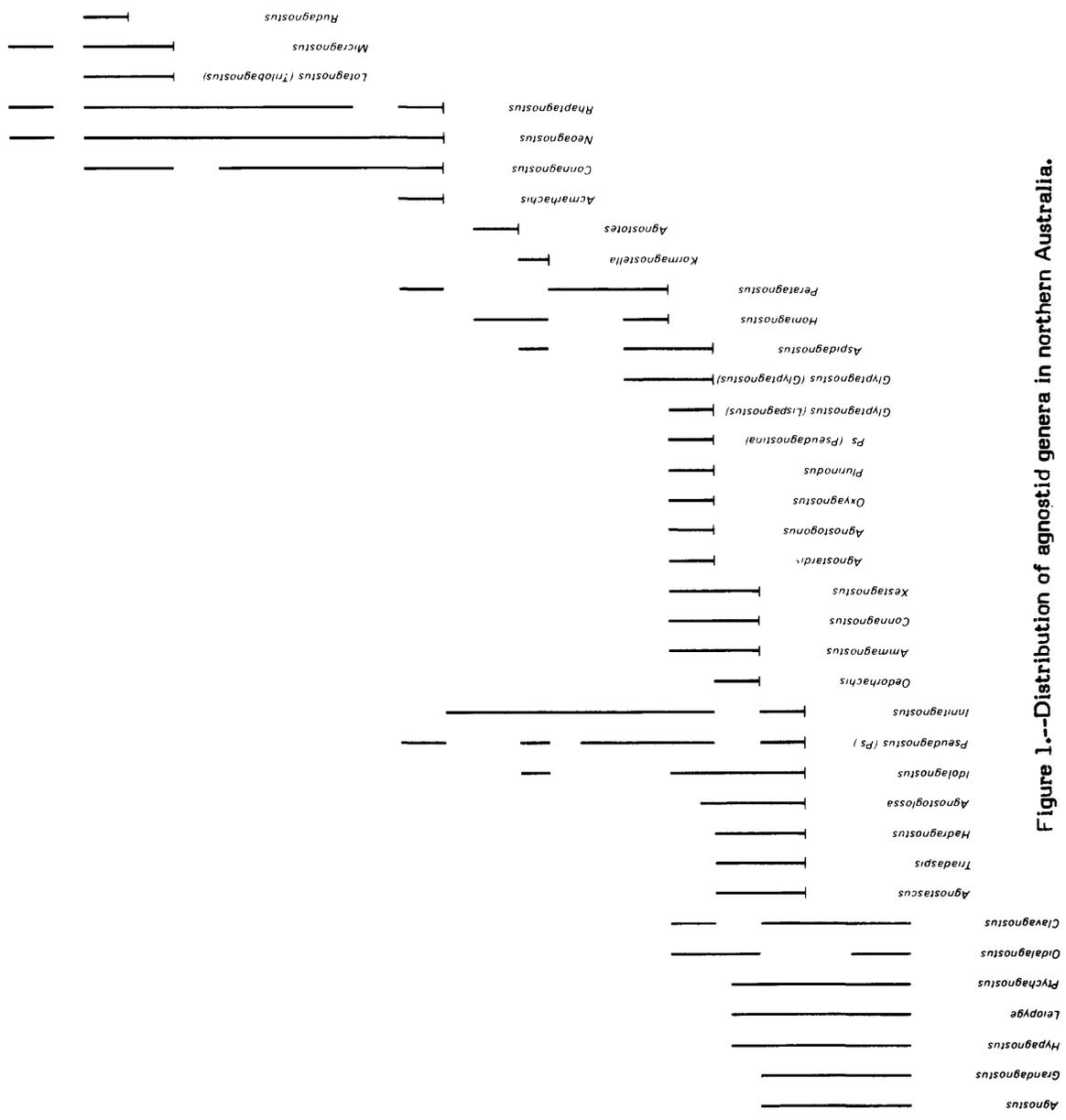


Figure 1.--Distribution of agnostid genera in northern Australia.

unclear. There are conceptual problems among homagnostoid genera: as originally conceived, Homagnostus is a genus of the Olenus Zone in northern Europe, but it has also been recorded from older and younger strata. In older rocks, its relationships with Agnostus require clarification, and in younger ones there is some morphological overlap with Micragnostus and Rudagnostus. Some Late Cambrian homagnostoids have constricted pygidial acrolobes and imitate Connagnostus (Diplagnostinae).

It is only in northern Australia (Opik, 1961a, 1963, 1967; Shergold, 1972, 1975, 1980, and in press) and Kazakhstan (Ergaliev, 1979) that agnostid sequences covering the entire Late Cambrian have been assessed. Only the late Dresbachian interval has been currently detailed in North America (Palmer, 1962). In northern Europe, agnostids of the Late Cambrian Acado-Baltic Province are commonly found only in the Agnostus pisiformis and Olenus Zones. Many Australian genera and species have been recognized in the monofacial Kir-Shabatky River section of southern Kazakhstan. Unfortunately, Ergaliev's scheme cannot be adequately judged because the systematic palaeontology on which it is based has not yet been published. The Australian multifacial sequences of the eastern Georgina Basin have been studied in detail. The biostratigraphy from the base of the Idamean up is controlled by measured lithological sequences. Because 37 of the 46 established Late Cambrian genera occur in the Georgina Basin, the sequences established there are used as standards here on figures 1 and 2.

Late Cambrian agnostid genera in the Georgina Basin (fig. 1) fall into two clear groups, as elsewhere in the world: Mindyallan and post-Mindyallan. The Mindyallan-Idamean faunal crisis (Opik, 1966) is a global event that corresponds to the base of the Pterocephaliid Biomere (Palmer, 1965a, b, 1979; Stitt, 1971, 1975). Unlike polymerid trilobites, which largely became extinct during this crisis, several agnostid lineages pass across the crisis interval, which occurs within the Glyptagnostus lineage.

Among Mindyallan agnostids (=early Dresbachian, Tuorian, Kushanian, and equivalents), tendencies are seen towards a thickening of the exoskeleton, effacement of exoskeletal morphology, the suppression of the anterior glabellar lobe, and modification of the pygidial axis, which often becomes deuterolobate.

The Mindyallan is a period of relatively stable lithosphere that began during the late Middle Cambrian (Paradoxides forchhammeri Stage and time equivalents). Crustal stability, together with climatic amelioration, was responsible for the wide spread of carbonate sediments. The proliferation of ephemeral, warm, shallow-water environments seems to have coincided with endemism among arthropod faunas; the accelerated morphological variation became necessary, presumably as a result of increased trophic competition.

Endemism has resulted in a proliferation of taxonomic nomenclature and confusion of taxonomic concepts. Mindyallan agnostids are not easy to classify, their evolutionary lineages are still poorly understood, and their spatial distribution is often concealed by synonymy. Because it is a continuation of a tectonic-stratigraphic regime that developed in the late Middle Cambrian, the Mindyallan Stage contains a significant proportion of agnostid genera originating in the Middle Cambrian, so much so that several authors have considered referring this stage in part (Daily and Jago, 1975) or in total (Rozova, 1964, 1968, 1970; Ergaliev, 1979) to the Middle Cambrian. Apart from pseudagnostine and glyptagnostine lineages, Mindyallan agnostids are sufficiently well known to be useful in international correlation.

An increase in lithospheric plate activity during post-Mindyallan time is demonstrated globally by renewed volcanism at plate margins, granitic and ultrabasic magmatic intrusion, a more widespread distribution of cooler and (or) deeper outer shelf sedimentary environments, a greater variety of depositional environments, and increased frequency of shoaling and emergence on the inner epicontinental shelves. Agnostid assemblages become less provincial in distribution, and morphologically more conservative. There is a wider incidence of thin-shelled, en grande tenue forms in which the caecal and diverticular systems are emphasised externally, and there is proliferation of deuterolobate taxa, particularly Pseudagnostinae. Because morphological diversity is less, fewer taxa have been erected, and taxonomic concepts are firmer, presenting fewer problems of interpretation.

Agnostina from this interval, which includes the Idamean through Paytonian of northern Australia, the Shidertan of the USSR, the late Dresbachian through early Trempealeauan of North America, and the Changshanian and Fengshanian of China, offer the best possibilities for biostratigraphic schemata and the establishment of an international biochronological scale.

Figure 1 also indicates the biochronological potential of Late Cambrian agnostid genera in northern Australia, where lineages based on Glyptagnostinae and Pseudagnostinae are currently used in local biostratigraphy. Potential is seen here for the Innitagnostus lineage; and that based on Lotagnostus may also prove useful, but its range is not yet firmly established worldwide. Significant events appear to be:

1. The incoming of the Pseudagnostinae, particularly Pseudagnostus (Pseudagnostus) in the early Mindyallan Erediaspis eretes Zone; an event that also occurs in the early Dresbachian Cedaria Zone of eastern USA and the Tuorian of northern China.



2. The entry of the Glyptagnostinae. Glyptagnostus stolidotus is also known in China (Kueichou), USSR (Yakutia), and North America (Alabama). Glyptagnostus reticulatus occurs widely (Kobayashi, 1949): in North America (Kobayashi, 1938, Palmer, 1962), Scandinavia (Westergård, 1947, Henningsmoen, 1958), England (Belt, 1867; Rushton in Taylor and Rushton, 1971), USSR (Rozova in Zhuravleva and Rozova, 1977; Tchernysheva, 1960), and China (Lu and others, 1965; Lu and others, 1980).
3. The beginnings of a lineage based on homagnostoids with constricted pygidial acrolobes referred to "Connagnostus" on figure 1. These are probably included elsewhere under the names Homagnostus or Geragnostus.
4. The radiation of the pseudagnostine genera Rhaptagnostus and Neoagnostus immediately following Irvingella. This event is so far most accurately documented in Australia.
5. The introduction of Micragnostus sensu stricto and Rudagnostus in the pre-Payntonian bifax/denticulatus and maximus/papilio assemblage zones. This pair of genera appears to be correlated to the level of Zones 5c-d in Scandinavia (Westergård, 1947; Shergold, 1975).

Specifically most useful at the present time, both biostratigraphically and biochronologically, are the Pseudagnostinae, a subfamily to which some 120 species have been assigned.

Pseudagnostine taxa range between early Mindyallan and latest Tremadocian (in Europe and South America). Figure 2 demonstrates the range of pseudagnostine taxa in the Georgina Basin. Analysis of the ranges of species group assigned to the genera Pseudagnostus, Rhaptagnostus, and Neoagnostus is rewarding, and is summarized below.

#### Pseudagnostus (Pseudagnostus)

##### Group of Ps. bulgosus Opik

Australia: Mindyallan, Erediaspis eretes to Glyptagnostus stolidotus Zones.

North America: early Dresbachian, Cedaria Zone.

USSR (Siberian Platform): Tuorian, Aagnostus pisiformis to Glyptagnostus stolidotus Zones.

##### Group of Ps. communis (Hall & Whitfield)

Australia: Idamean, Stigmatocia diloma to post-Idamean, Peichiashania tertia/P. quarta Assemblage-Zone.

North America: late Dresbachian, Aphelaspis to early Trempealeauan Saukia Zone.

USSR (Yakutia): late Tuorian, Glyptagnostus reticulatus to Shidertan Plicatolina perlata Zone.

Asia (N. China and Korea): Paishanian, Chuangia Zone.

#### Group of Ps. cyclopyge (Tullberg)

Australia: late Mindyallan, Glyptagnostus stolidotus to post-Idamean, Peichiashania secunda/Prochuangia glabella A-2.

USSR (Central Kazakhstan): late Tuorian, Glyptagnostus reticulatus to Shidertan, Irvingella Zone.

North Europe: Zones of Parabolina spinulosa/Orusia lenticularis to Peltura scarabaeoides.

Asia (North China, South Korea, Afghanistan): Kushanian?, Blackwelderia paraonai to Changshanian, Eochuangia Zone.

#### Rhaptagnostus

##### Group of R. convergens (Palmer)

Australia: post-Idamean, Wentsuis iota/Rhaptagnostus apsis Assemblage Zone to pre-Payntonian, R. clarki maximus/R. papilio Assemblage Zone.

North America: Trempealeauan, Saukia Zone (Saukiella pyrene Subzone).

USSR (Kazakhstan): Shidertan, Lotagnostus trisectus/Peltura Zone.

Asia (North China): late Changshanian, Kaolishania Zone.

##### Group of R. clarki (Kobayashi)

Australia: post-Idamean, Peichiashania tertia/P. quarta Assemblage Zone to Payntonian, Neoagnostus quasibilobus/Tsinania nomas Assemblage Zone.

North America: Trempealeauan, Saukia Zone (Saukiella pyrene? S. serotina Subzones); Cordylodus proavus Zone? Mexico.

USSR (Kazakhstan): Shidertan? to initial Tremadocian?

Asia (China, North and South Korea): late Changshanian, Kaolishania Zone to Fengshanian, Tsinania Zone.

## Neoagnostus

### Group of N. clavus (Shergold)

Australia: post-Idamean to pre-Payntonian, Wentsuia iota/Rhaptagnostus apsis through R. clarki maximus/R. papilio Assemblage Zones.

North America (British Columbia): early Franconian, Elvinia Zone.

USSR (Kazakhstan): Shidertan, Irvingella through Peltura Zones.

Asia (North China, South Korea): late Changshanian, Kaolishania Zone.

### Group of N. canadensis (Billings)

North America (Canada): Late Cambrian, Hungaia fauna.

### Group of N. araneavelatus (Shaw)

Australia: post-Idamean, Wentsuia iota/Rhaptagnostus apsis to pre-Payntonian, R. bifax/Neoagnostus denticulatus Assemblage Zones.

North America (Vermont): Missisquoia Zone.

Asia (South Korea): late Changshanian, Kaolishania Zone.

### Group of N. bilobus (Shaw)

Australia: Payntonian, Neoagnostus quasibilobus/ Tsinania nomas Assemblage Zones.

North America (Vermont, British Columbia): Early Ordovician, Missisquoia through Kainella/ Evansaspis Zones.

South America (Argentina, Bolivia): early Tremadocian, Parabolina argentina Zone.

Asia (Southwest China, North China): Fengshanian to Wanwanian.

Acknowledgment: This paper is published with the approval of the Director, Bureau of Mineral Resources, Canberra, Australia.

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## 59. PALEOECOLOGY OF A LOWER CAMBRIAN ARCHAEOCYATHID INTERREEF FAUNA FROM SOUTHERN LABRADOR

By

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Reefs and similar mound-like carbonate buildups preserved in the geologic record have been studied extensively (for example Wilson, 1975); yet, studies of the organisms and associated sediments have most often been restricted to the reef proper. Few studies exist in which either modern or fossil reef faunas were taxonomically or ecologically compared to their associated off-reef faunas. There is perhaps no better place to begin a detailed study of interreef communities than in the Early Cambrian where Archaeocyathids were the first organisms to construct what might be termed a modern reef structure (Copper, 1974), exclusive of course of the pre-Paleozoic stromatolitic mounds.

### PALEOENVIRONMENT

In general, reefs create a physical obstruction to previous circulation patterns as they develop and grow vertically (Lowenstam, 1950; James, 1977); thus, the growth of a reef can promote changes in the local physical-sedimentological realm. James (1977) pointed out that as a reef grows it develops a distinctive biological zonation that appears to be correlated with changes in the associated sedimentological regime of the reef. Given this information, one would assume that some kind of change would also have been produced in the interreef organism-sediment associations as well. These effects would most likely occur along a gradient, being more pronounced near the reef and gradually diminishing away from the obstruction. Such physical changes may be small and yet still have a significant effect on the local biological habitat.

Archaeocyathid patch reefs of the lower Forteau Formation, southern Labrador (fig. 1), developed in the relatively quiet-water environment of the Lower Cambrian epiherc sea. Although the archaeocyathid patch reefs stood 1-3 m above the sea floor, it is obvious from the external morphology of the individual archaeocyathids and the number of overturned and

restored colonies that the reefs encountered higher energy conditions as they grew. Thus, there archaeocyathid patch reefs apparently created many small, discontinuous obstructions to currents and waves. Differences in the distribution of sediments around these complexes appear to be related to changes in the physical environment resulting from the presence of the reefs. Such sedimentological and inferred physical differences are exemplified in the interreef environment around the Fox Point Cliff Complex.

Sediments on the southwest flank of the Fox Point Cliff Complex are composed of large, predominately unbroken shells that occur in fine silts. The undisturbed silts preserved on the tops of some of these shells indicate that the current and wave energies affecting this flank were not strong. The organisms appear to have lived in a silty, quiet but well-oxygenated environment. On the other hand, on the northeast flank of the Fox Point Cliff Complex indicate a somewhat higher energy environment. The skeletal grains comprising these sediments are broken, smaller, better sorted, and contain less silt than those on the southwest flank. Because these grainstones have been interpreted as episodic storm deposits, continual silt accumulation is not indicated. The surface of the storm-deposited sediments appear to have been exposed to extensive bioturbation, and, in some cases, possible slight lithification prior to the next storm event. The lack of continual silt accumulation on this flank and the occurrence of higher energy storm deposits suggest that both constant and episodic storm-generated waves and currents were stronger on the northeast flank of Fox Point Cliff Complex.

### FAUNAL DISTRIBUTION

Differences in the distribution of sediments around the Fox Point Cliff Complex is accompanied by an associated difference in the composition of the faunal assemblages found within and on these sediments. Higher silt abundance of silts on the southwest flank of the Fox Point Cliff Complex

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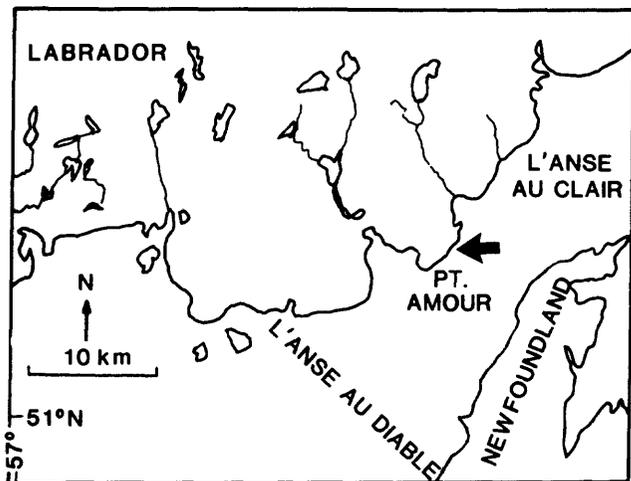


Figure 1.--Index map showing location of study area in southern Labrador, Canada.

probably excluded genera such as *Discinella* and *Hadrotreta*, which do occur on the northeast flank. These small organisms are filter feeders, a life habit that requires clear, well-agitated waters in order to keep their filter-feeding apparatus from being clogged. The organisms that dominated the more silt-rich, quiet environments were: *Hyalithes*, an epifaunal deposit feeder; *Stenothecoides*, an epifaunal suspension feeder; and *Obolella*, an epifaunal filter feeder. The packstone facies on the southwest flank differ distinctly from those on the northeast flank in both lithofacies and biofacies. These differences might be related to the presence of the reef, which apparently brought about changes in the local environment.

#### CONCLUSIONS

The physical changes produced by these archaeocyathid complexes on their surrounding environment appear to have had other effects on the interreef faunas. The two distinctly different faunas associated with the environments around these patch reef complexes show a similar change in dominance diversity ( $d$ ) with distance from the complex (fig. 2a). The faunal assemblages on the flanks of each complex illustrate a general decrease in the abundance of dominant species with distance from the complex or a more equitable distribution of individuals per species. However, the faunal composition of each assemblage does not change with distance from the complex. Thus, the faunal composition might have been controlled by major differences in the physical conditions that produced the two environmental regimes. The gradual lowering of the dominance diversity with distance from the complex could be

related to a subtle but gradual change in the marine environment. There is no obvious sedimentological evidence for this presumed change in the local physical environment. There is, however, a distinct change in the distribution of individuals per species in each interreef faunal assemblage (fig. 2b). In each case a single taxon is most abundant close to the complex (making up 50-86 percent of the assemblage), but its abundance decreases with distance from the reef. The second and third most abundant taxa close to the reef make up a substantially smaller portion of the assemblage (commonly less than 20 percent), but, conversely, increase in abundance farther from the complex. The remaining part of the fauna represents those genera that remain in low abundance (usually less than 2 or 3 percent) and showed no significant changes in number with distance from the complex. Thus, the high degree of dominance close to the reef appears to produce a geometric distribution of the individuals per species.

Faunal assemblages in which the distribution of the individuals per species approaches a geometric distribution are indicative of physically disturbed habitats (Whittaker, 1975). The distribution of interreef faunas living close to the patch reef complexes implies, therefore, that this could have been a physically disturbed environment. The decrease in dominance farther from the complex suggests that these areas could have been under less physical stress. Waves and currents impinging on the windward side of a reef should be most intense next to the reef and decrease in intensity farther from the reef. Currents diverted by a small patch reef would flow over and around this obstruction, thereby creating a zone of higher physical energy around the reef. In each case examined, the interreef faunal distributions could be related to a higher physical disturbance directly around the reef that decreases with distance from the reef. Thus, changes in the local physical-sedimentological environment produced by the reef appear to have affected the ecological structure of the interreef faunas.

Acknowledgments.--I thank Dr. A. R. Palmer for his guidance and support in the formative stages of this project, and Dr. P. W. Bretsky for his suggestions in the later stages of the study. Dr. J. Smoot provided useful discussion of the sedimentology and environmental interpretation, and Dr. George Lynts critically reviewed the manuscript. Financial support for this research was provided by grants held by Dr. A. R. Palmer.

## Fox Point Cliff Complex

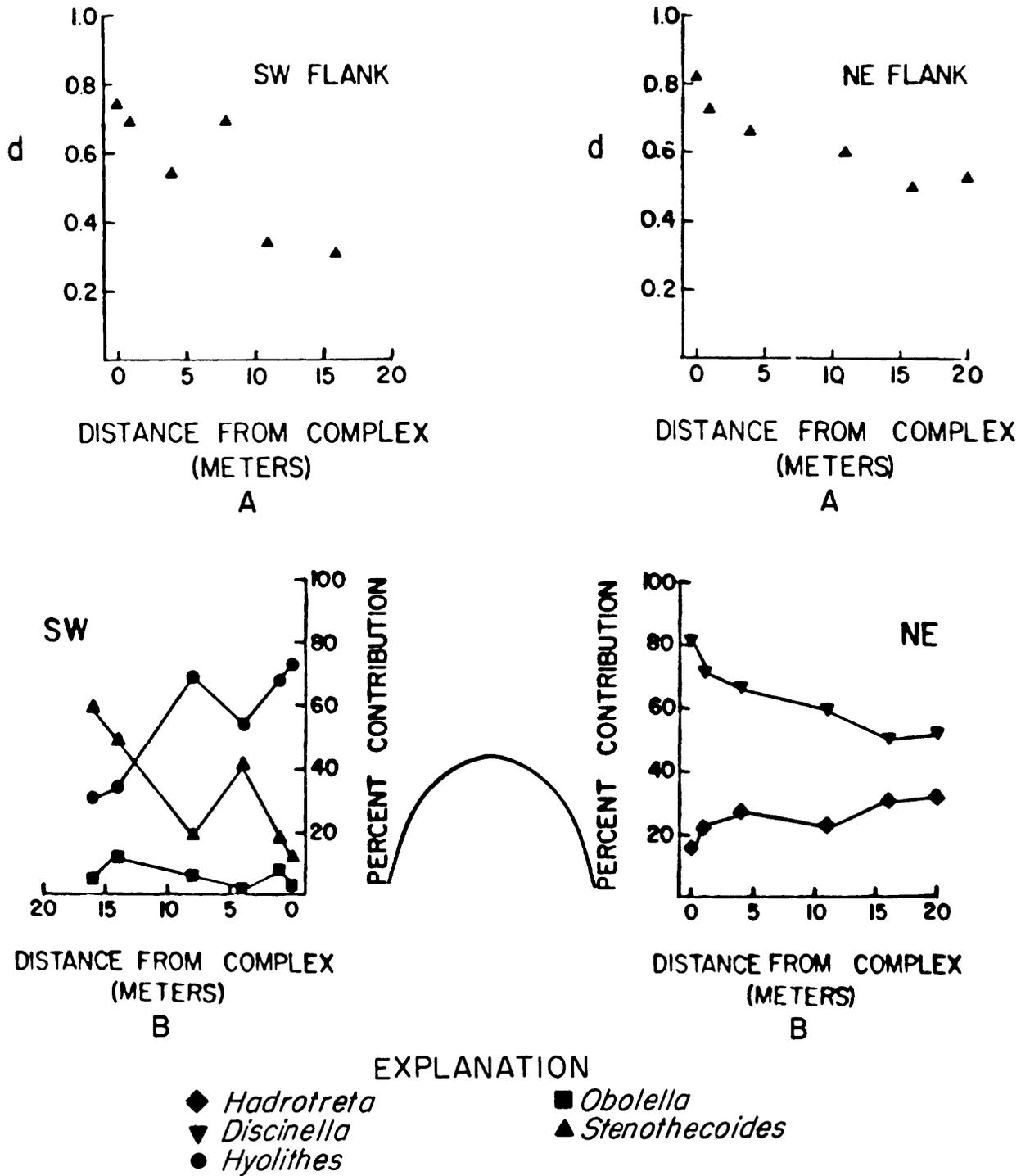


Figure 2.--A, Dominance diversity (d) gradient for the northeast and southwest flanks of the Fox Point Cliff Complex illustrate a decrease in dominance with distance from the complex. B, Percent contribution of those species making up a dominant portion of the faunal composition on the northeast and southwest flanks of the Fox Point Cliff Complex.

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## 60. DIVERSITY AND EVOLUTIONARY PATTERNS OF CAMBRIAN ECHINODERMS

By

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Cambrian echnioderms represent the initial stage of a major evolutionary radiation of this phylum into several different ways of life in shallow-water marine environments. At least 10 classes and 38 genera are present in the fossil record during the Cambrian, starting in the Fallotaspis Zone just above the base of the Early Cambrian and extending to the end of the Late Cambrian (Sprinkle, 1976, 1980). Compared to large successful groups such as the trilobites in the arthropods, echinoderms are a much smaller, less dominant, but highly varied phylum in the Cambrian fossil record. They had a plastic body form and tried a variety of different ways of life in the Cambrian, thus adding to their diversity at the class and order levels. However, no single body-plan or way of life became dominant until later in the record (Middle Ordovician), so that generic and specific diversity within classes is rather low. Several models for the early diversification of metazoans have tried to explain this type of pattern (Valentine, 1969; Sepkoski, 1979).

Three or perhaps four classes of echinoderms appeared in the Early Cambrian: helicoplacoids (Durham, 1967), eocrinoids (including the lepidocystoids of Durham, 1968; see Sprinkle, 1973), edrioasteroids (including the camptostromoids of Durham, 1966, based on oral commun. from Kraig Derstler, 1978), and perhaps homoiostelean (see Derstler, 1975). Almost all of these forms are known from isolated occurrences in eastern or western North America. Diversity was low, with helicoplacoids (three genera and six species; see Durham, 1967) being the most diverse.

Echinoderms were more diverse and widespread in the Middle Cambrian with six to eight classes present: eocrinoids (see Sprinkle, 1973), crinoids (Sprinkle and Moore, 1978), edrioasteroids (probably including the cyclocystoid described by Henderson and Shergold (1971), based on oral commun. from Andrew Smith, 1981; see also Cabibel and others, 1958; Bell and Sprinkle, 1978), homostelean (Termier and Termier, 1973), stylophorans (Ubaghs, 1968), ctenocystoids (Sprinkle and Robison, 1978), possible homoiostelean (Kraig Derstler, oral commun., 1980), and possible holothurians (see Durham, 1974). Middle Cambrian occurrences of complete specimens became more widespread, including many in western North America and in central and western Europe, plus a few

in other areas. However, diversity still remained low except for eocrinoids (especially the genus Gogia which now has 11 named species plus several more unnamed at present; see Sprinkle, 1973; Durham, 1978).

Echinoderms became somewhat less diverse but more widely distributed in the Late Cambrian where four classes are known; two others (crinoids and perhaps holothurians) also must have been in existence because of earlier and later occurrences, but have not been found. Eocrinoids (Sprinkle, 1973), stylophorans (Ubaghs, 1963, 1968), homoiostelean (Ubaghs, 1963; Bell and Sprinkle, 1980), and edrioasteroids (Sprinkle and Strimple, unpub. data) are present in scattered occurrences in western, central, and eastern North America, western Europe, North Africa, and Siberia. Diversity was again relatively low for most classes. However, (1) many forms have either thin plates or large, tiny-plated, central areas, and (2) thick-bedded carbonates were widespread in many areas; both of these factors were unfavorable for the preservation of complete specimens. These factors have probably reduced the apparent diversity in the Late Cambrian, although many occurrences of undescribed echinoderms (both rare and complete specimens and disarticulated plates) are also known.

Although some echinoderm localities throughout the Cambrian have yielded hundreds or even thousands of specimens, diversity of echinoderms is quite low at most localities, with only one, two, or rarely three echinoderm genera and species occurring together (see Sprinkle, 1976). Most echinoderm species have only a local geographic range, and have been found at only a few nearby localities of the same formation. Stratigraphic ranges are poorly known because of limited collecting, but in general appear to be short. Most of these early echinoderms were rather generalized suspension or detritus feeders; no echinoderm herbivores or carnivores were present until the Early or Middle Ordovician (Sprinkle, 1976). Many Early and Middle Cambrian echinoderms had primitive morphology with numerous irregular or imbricate thecal plates, sutural pores for respiration, only the ambulacral system showing any pentamerous symmetry, a short multiplated holdfast for attachment to objects on the sea floor in medium-level suspension feeders,

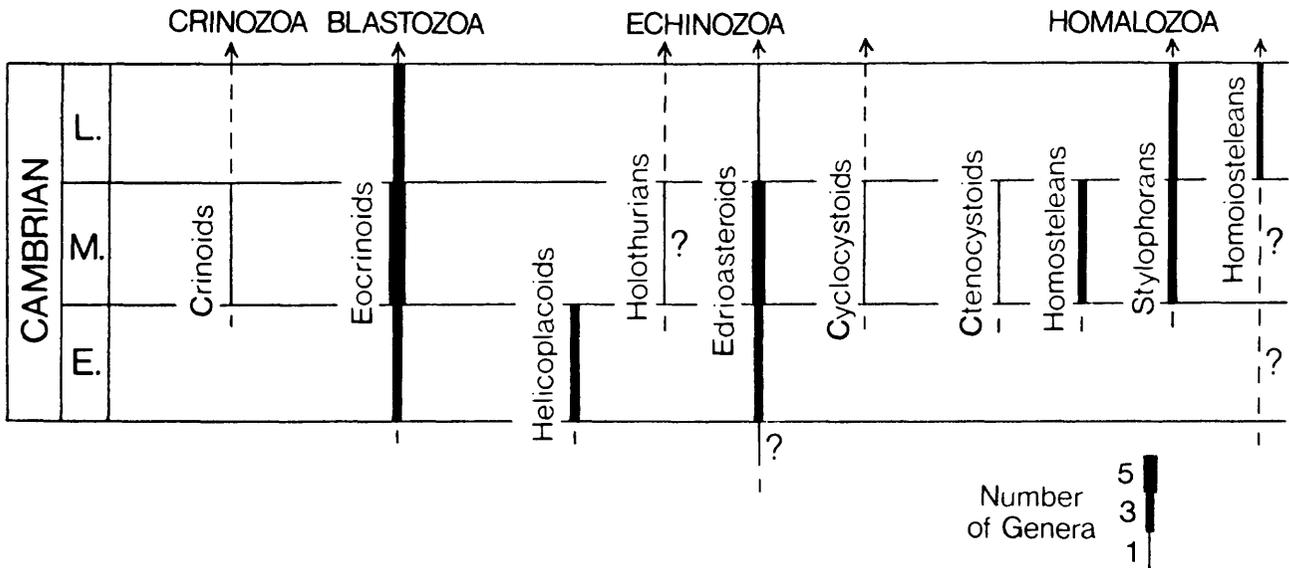


Figure 1.--The initial radiation of echinoderms in the Cambrian showing classes present with their generic diversities (modified from Sprinkle, 1980). Recent work (Andrew Smith, oral commun., 1981) indicates that the single Cambrian cyclocystoid reported by Henderson and Shergold (1971) may in fact be an edrioasteroid. E, Early Cambrian; M, Middle Cambrian; L, Late Cambrian.

and rather simple food-gathering appendages (Sprinkle, 1980). The more successful echinoderm classes made gradual improvements in morphology in the Middle and Late Cambrian; these included reducing the number of thecal plates and arranging them in circlets with better pentamer symmetry, eliminating the sutural pores, and in eocrinoids developing a longer columnal-bearing stem for attachment (Sprinkle, 1973).

The Cambrian record of echinoderms represents the initial stages of a major radiation of echinoderms in the shallow-water marine environment. Four of the five echinoderm subphyla (all except Asterozoa) probably crossed the Precambrian-Cambrian boundary as separate lineages (Sprinkle, 1976) and began to diversify. New classes appeared suddenly in the record without obvious ancestors, and many of these classes were local in extent, were rather short-lived, and had very low diversity (see fig. 1). These features may indicate that one or more types of rapid evolutionary change or the initial development of mineralized skeletons may have produced this pattern (see Sprinkle, 1980). The Echinozoa and Homalozoa (fig. 1, center and right side) produced three or four classes each of attached or stationary low-level suspension feeders and mobile detritus feeders. The Crinozoa and Blastozoa (fig. 1, left side) produced only one class each of medium-level attached suspension feeders. None of these classes became dominant during the Cambrian (Sprinkle, 1980), and the largest class (eocrinoids) has only about 13 Cambrian genera worldwide (Sprinkle, 1976), or about 34 percent of the known Cambrian echinoderm genera. Several additional classes with new designs and ways of life (such as

rhomberans, asteroids, and echinoids) appeared from unknown ancestors in the Early and Middle Ordovician; some of these classes may originally have evolved in the Late Cambrian but have not yet been found here.

This initial diversification of echinoderms closely matches the two or three-stage model for shallow-water skeletized metazoans proposed by Sepkoski (1979, 1980). The more successful Cambrian echinoderm classes (eocrinoids, helicoplacoids) probably would represent part of his "Cambrian fauna"; other echinoderm classes (such as crinoids, edrioasteroids, and stylophorans) became more successful in the Ordovician and later periods and represent part of his "Paleozoic fauna" (Sepkoski, 1980). Some echinoderm classes missing from the Cambrian record (such as echinoids and asteroids) did not become abundant until much later, and would be included in his "modern" fauna. This may imply that early-appearing "fast" groups peaked early and were then replaced by later-appearing "slow" groups that had developed advanced morphology while subordinate to more successful "fast" groups. Although Sepkoski has argued that the exact time of origin and early history of a group are not important factors in determining its later history and to which fauna it belongs (1979, and oral commun., 1980), the Cambrian fossil record of echinoderms hints that these factors may well be important and perhaps critical.

In the next few years, important information on Cambrian echinoderm evolution probably will come from new collections and revisions of Early and Late Cambrian forms that are not well known at present. Several newly discovered Late Cambrian faunas are

- now under study (Sprinkle and Strimple, unpub. data; Bell and Sprinkle, 1980), and others probably will be found. Hopefully, this work will greatly increase our knowledge of echinoderms from these intervals, which has been held back by lack of collecting and unfavorable facies conditions. Work by K. L. Derstler and others on Early Cambrian echinoderms will add additional information about this critical early part of the echinoderm fossil record.
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# 61. THE CAMBRIAN-ORDOVICIAN TRANSITION IN THE BEAR RIVER RANGE, UTAH-IDAHO: A PRELIMINARY EVALUATION

By

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Uppermost Cambrian and Lower Ordovician rocks in southeastern Idaho and northern Utah (fig. 1) are assigned to the St. Charles Formation and the Garden City Formation (Mansfield, 1927; Williams, 1948). Biostratigraphy of shelly fossils from the Garden City Formation was studied by Ross (1949, 1951, 1953, 1968), who proposed (1949) a zonation consisting of 12 assemblage zones lettered A to L based primarily on trilobites. Shelly fossils in the St. Charles consist of upper Franconian trilobites, brachiopods, and gastropods from the Worm Creek Quartzite Member, the lower member of the St. Charles (Williams and Maxey, 1941; Lochman and Hu, 1959). Known fossils from the upper unnamed dolostone member of the St. Charles consist of algal stromatolites and a few mollusks assigned to the Upper Cambrian Trempealeau Stage (John Pojeta, Jr., J. E. Repetski, and M. E. Taylor, unpub. data). The sparsity of shelly fossils from the upper St. Charles, and especially the absence of trilobites, lent caution to Ross' (1951, p. 6) interpretation of the Cambrian-Ordovician boundary in the Bear River Range, although, in the absence of faunal data, the boundary has usually been placed at the St. Charles-Garden City contact as a matter of convenience (Mansfield, 1927; Williams and Maxey, 1941; Williams, 1948; Ross, 1949, 1951; Oriel and Platt, 1980).

The shelly fossil zonation of the Garden City Formation has been widely applied in North America (for example, Hintze, 1951, 1952; Whittington, 1968; Norford, 1969; Fisher, 1977). Ross (1949, p. 481) however, recognized the uncertain validity of trilobite Zone A, and the correlation of Garden City trilobite Zone A with other areas has proved difficult (Hintze, 1952, p. 5; Winston and Nicholls, 1967, p. 72; Norford, 1969, p. 2; Taylor and Halley, 1974, p. 6-8; Stitt, 1977, p. 25). The difficulty arises primarily because trilobites are relatively rare and nonsilicified in the lowest part of the Garden City.

This report is a brief summary of results of a team project to reevaluate the lithostratigraphy, conodont and trilobite biostratigraphy, and magnetostratigraphy of the upper St. Charles Formation and the lower Garden City Formation in the Bear River Range. Principal objectives are (1) to

locate biostratigraphically the Cambrian-Ordovician boundary, (2) to determine the age and correlation of trilobite Zone A of Ross, and (3) to determine whether paleomagnetic signatures are present in the rocks that may be potentially useful for magnetostratigraphic correlation. To achieve these objectives, the upper 60-75 m of the St. Charles and lower 50 m of the Garden City were measured and sampled for conodonts and shelly fossils at four localities on the western limb of the Logan Peak syncline (Williams, 1948; Oriel and Platt, 1980), Bear River Range, northern Utah and southeastern Idaho (fig. 1). The four sections studied (fig. 1) are near Ross' (1949, 1951) localities at Franklin Basin and Hillyard Canyon, Franklin County, Idaho and Blacksmith Fork and Green Canyons, Cache County, Utah. The Green Canyon section (fig. 1) has a fault contact between the St. Charles and Garden City Formations and is not discussed here (see Landing, 1981). All sections yielded abundant conodonts, but the Franklin Basin section contained the richest trilobite assemblages in the lowermost part of the Garden City.

## LITHOSTRATIGRAPHY

The upper 75 m of the St. Charles Formation consists of medium- to dark-gray dolostone that is medium to massively bedded. Dark-greenish-brown chert commonly occurs as irregularly shaped nodules and interconnecting stringers. Original depositional textures and sedimentary structures are commonly preserved on weathered surfaces. These show the original sediment to have included bioclastic grainstones and wackestones composed of molluscan skeletal debris with varying amounts of mud matrix; boundstone, including high-relief hemispherical stromatolites as much as 30 cm in diameter, thrombolites, and oncolites; and less commonly, parallel laminated fine-grained sediments that may be of algal-mat origin. Some hemispherical stromatolites are constructed of weakly developed to moderately well developed laminae, whereas others are irregularly shaped and grade into nonlaminated thrombolites which contain coarse "zebra fabric" fenestrae. Some stromatolitic beds grade upwards to white dolostone

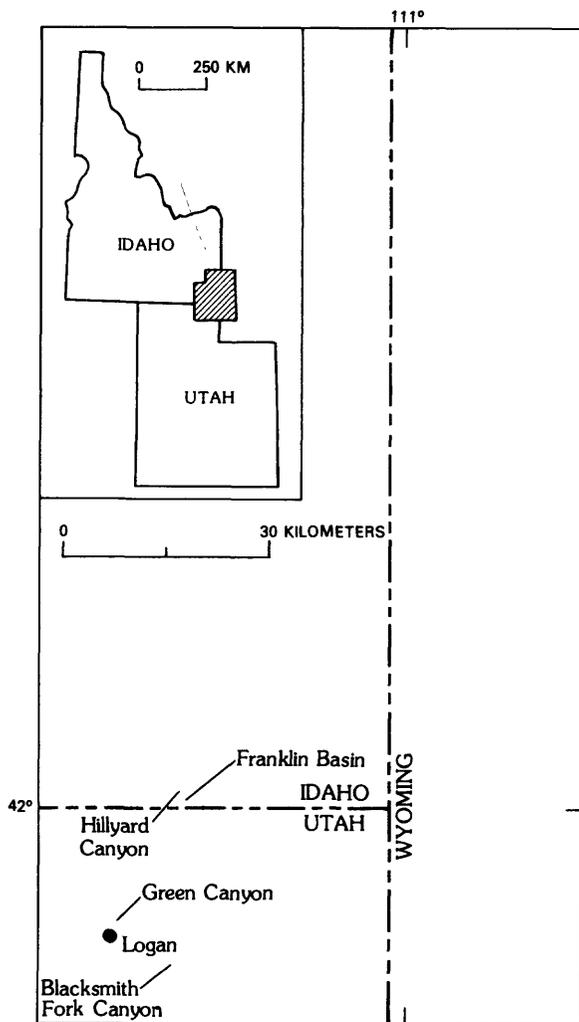


Figure 1.--Index map showing location of measured sections and study area.

that lacks a clearly defined depositional fabric. Some channel fills show relief as great as 0.6 m.

Stromatolitic units interbed with dark-gray dolostone that shows abundant bioturbation. These rocks are mottled with different shades of gray, and some contain abundant white dolomite-filled burrows as much as 0.5 cm in diameter.

The upper St. Charles contains some grainstones in beds 5-15 cm thick. The beds are composed of peloids, composite clasts, ooids, and coated grains. The matrix is white dolomite.

Fenestral fabric (or "zebra fabric") increases in frequency and size of void-fills toward the top of the St. Charles. Individual fenestrae are irregularly shaped, cut across depositional fabrics, and are as much as 25 cm in maximum cross-sectional dimension. Fenestrae are filled with white blocky dolomite.

White dolomite is common in the upper St. Charles Formation. It occurs as fillings in large secondary cavities, as burrow fillings in mudstone, and as cement in bioclastic and oncolitic grainstones.

The contact between the St. Charles Formation and the overlying Garden City Formation is sharp. In outcrops with continuous exposures, the contact is knife-edged and goes from massively bedded, coarsely crystalline, medium-gray dolostone with blocky white dolomite filled voids below, into thinly bedded lime mudstone-wackestone that weathers medium to light gray or into medium weathering, finely crystalline, poorly laminated light brown dolostone. At Hillyard Canyon the lower 14.7 m of the Garden City consists of poorly exposed dolomitic sandstone and arenaceous dolostone with varying amounts of fine-grained quartz sand. Approximately 20 cm of arenaceous dolostone occurs at the base of the Garden City Formation in the Franklin Basin section.

Lithoclastic-bioclastic grainstones, lime mudstones-wackestones, and intraformational limestone conglomerates are the predominant lithologies of the Garden City Formation. The formation is evenly bedded, in beds 5-25 cm thick. In the Blacksmith Fork section, the lower 5 m of the Garden City is dolomitized. However, the presence of intraformational conglomerate with a trilobite skeletal matrix shows that the dolostone belongs to the Garden City rather than the underlying St. Charles Formation.

The large white dolomite-filled solution cavities in the uppermost beds of the St. Charles, the bleaching of the same upper beds from dark gray to light gray, and the sharp contact with the overlying, thinly bedded Garden City limestones are physical evidence of disconformity between the two formations. This interpretation, and faunal data discussed below, support the conclusions of Mansfield (1927) and Williams (1948) that a disconformity exists at the St. Charles-Garden City contact.

## TRILOBITES

New trilobite collections were made to clarify the taxa present in the stratigraphic interval previously assigned to Zone A of Ross (1951). At Franklin Basin a limestone bed 1 foot (0.3 m) above the base of the Garden City yielded the following trilobite species: *Symphysurina brevispicata* Hintze, *Symphysurina* cf. *S. cleora* (Walcott), *Symphysurina uncaspicata* Hintze, *Symphysurina*(?) n. sp., *Hystricurus millardensis* Hintze, *Clelandia texana* Winston and Nicholls, *Clelandia utahensis* Ross, *Bellefontia*(?) sp., and *Highgateella*(?) sp. Most of the species also occur in trilobite Zone B of Hintze (1952, p. 7) from the House Limestone in the southern House Range, Utah.

Stitt revised the Symphysurina Zone after detailed studies of trilobite ranges in the Signal Mountain Limestone of southwestern Oklahoma (Stitt, 1977, p. 32-36). Stitt divided the Symphysurina Zone into a lower, S. brevispicata Subzone which is based on the lowest occurrence of S. brevispicata, Highgatella cordilleri (Lochman), and Symphysurina sp. A of Ross; and an upper S. bulbosa Subzone, the base of which is defined by the lowest occurrence of S. bulbosa. The top of the S. bulbosa Subzone is not well defined, but it occurs below the Bellefontia-Xenostegium Zone.

The trilobite assemblage from the lower 1 foot (0.3 m) of the Garden City (listed above) correlates with the S. brevispicata Subzone of Stitt (1977). However, the presence of Clelandia texana indicates the uppermost part of the subzone. Clelandia texana is known from only the uppermost part of the subzone in Oklahoma (Stitt, 1977) and central Texas (Winston and Nicholls, 1967).

The Franklin Basin section yielded Symphysurina sp. 11 feet (3.4 m) above the base of the Garden City. The specimen is similar to "unassigned pygidium no. 2" of Stitt (1977, pl. 6, fig. 7), which he assigned to the S. bulbosa Subzone. This similarity suggests that additional taxonomic study of the Symphysurina species complex may yield increased understanding of the details of biostratigraphic correlation within the upper part of the Symphysurina Zone.

Xenostegium franklinense Ross was collected 32 feet (9.8 m) above the base of the Garden City Formation at Franklin Basin. At 41.5 feet (12.6 m) above the base, Bellefontia acuminiferentis Ross, Symphysurina woosteri Ulrich, Clelandia sp., and Remopleuridella sp. were collected. This assemblage is characteristic of trilobite Zone B of Ross.

We conclude that trilobite Zone A of Ross at Franklin Basin corresponds to the upper part of the Symphysurina brevispicata Subzone and the S. bulbosa Subzone of the Symphysurina Zone of Stitt (1977) and that the lower part of the Symphysurina brevispicata Subzone is missing because of the hiatus between the Garden City and St. Charles Formations. This conclusion is corroborated by the absence of the Clavohamulus hintzei and Hirsutodontus simplex Subzones of the Cordylodus proavus Zone discussed below.

#### CONODONTS

A conodont zonation of the Cambrian-Ordovician transition has been developed by Miller (1980) in the Notch Peak Formation and lower House Limestone of the Pogonip Group in the Ibex area of western Utah. Younger conodonts have been studied by Ethington and Clark (1971) from the same area. Conodonts are sparse in the upper part of the St. Charles Formation (commonly less than 5 elements per kilogram), but some of Miller's (1980) and Ethington and Clark's (1971) faunal units can be recognized. Detailed ranges

of conodonts in the upper St. Charles and lower Garden City Formations were given by Landing (1981); results are summarized below and in figure 2.

In the Blacksmith Fork Canyon section (fig. 1), the Cordylodus proavus Zone occurs through the upper 14 m of the St. Charles Formation. The zone is locally recognized as the stratigraphic interval between the lowest occurrence of Cordylodus oklahomensis s.f. and the lowest occurrence of taxa assigned to conodont Fauna C in the lowest beds of the overlying Garden City Formation. Teridontus nakamurai is restricted to the Cordylodus proavus Zone in the Blacksmith Fork section.

The lowest beds of the Garden City Formation at Blacksmith Fork contain Cordylodus angulatus s.f.. Approximately 1.5 m above the base of the Garden City is the lowest occurrence of "Acanthodus" lineatus, "Oistodus" triangularis s.f., Acanthodus uncinatus s.f., Loxodus bransoni, "Paltodus" bassleri, "Paltodus" spurius, and Semicontoidus iowensis. The assemblage is assigned to conodont Fauna C of Ethington and Clark (1971) and occurs through the lower approximately 28 m of the Garden City Formation.

At the Hillyard Canyon and Franklin Basin sections (fig. 1), the upper 5-7 m of the St. Charles Formation contains conodont species assigned to the Clavohamulus elongatus Subzone of the Cordylodus proavus Zone (fig. 2). The total thickness of the C. proavus Zone is 30-40 m in the Franklin Basin and Hillyard Canyon sections, but the lower boundary is poorly known because of low specimen yield from samples.

Conodonts from the lowest part of the Garden City Formation at Franklin Basin and Hillyard Canyon are considerably younger than those from the underlying uppermost St. Charles Formation and are somewhat older than the lowest Garden City faunas at Blacksmith Fork and Green Canyons. The oldest conodont fauna of the Garden City comprises some of the characteristic conodonts reported from conodont Fauna C of Ethington and Clark (1971), although here it is interpreted as upper Fauna B. Conodont Fauna C was originally defined (Ethington and Clark, 1971, fig. 2) by the association of thirteen form species. The lowest conodont fauna from the Garden City Formation lacks Oistodus sp. of Ethington and Clark (1971), Loxodus bransoni Furnish, Clavohamulus densus Furnish, "Paltodus" spurius Ethington and Clark, Chosonodina herfurthi Müller, and Drepanodus spp. s.f. These taxa appear higher in the Garden City Formation, where they are associated with most of the forms first appearing in the lower part of the formation. This lowest fauna of the Garden City lacks a complete component of species comprising Fauna C in its original formulation, and this distinctiveness is here emphasized by its designation as "upper Fauna B" (fig. 2). Miller's (1978) definition of the base of an "upper Fauna B" marked by the lowest occurrence of

System	Stage	Trilobites	Conodonts	House Range, Utah Hintze (1973) Hintze, Miller, and Taylor (1980)	Bear River Range, Utah and Idaho (This report)	Bear River Range, Utah and Idaho Ross (1949)	House Range, Utah Hintze (1951)		
Ordovician		<i>Leiostegium-Kainella</i>	Fauna D	Fillmore Formation		Zone D	Zone D		
		<i>Paraplethopeltis</i>	Fauna C	House Limestone	C,T Garden City Formation	Zone C	Zone C		
		<i>Bellefontia-Xenostegium</i>			Zone B	Zone B			
	<i>Symphysurina</i>	<i>Symphysurina bulbosa</i>	upper part Fauna B	C,T disconformity	Zone A		Upper Cambrian trilobites listed		
		<i>Symphysurina brevispicata</i>	lower part						
	<i>Missisquoia</i>	<i>Missisquoia typicalis</i>	<i>Cordylodus proavus</i>	<i>Clavohamulus elongatus</i>	Lava Dam Member	C	not studied	Upper Cambrian trilobites listed	
				<i>Fryxellodontus inornatus</i>		C			
	<i>Missisquoia depressa</i>	<i>Proconodontus</i>	<i>Hirsutodontus hirsutus</i>	Notch Peak Formation	Red Tops Member	C	carbonate member	C	
			<i>Cambroistodus minutus</i>			C			
	Cambrian	Trempealeauan	<i>Saukiella</i>	<i>Corbinia apopsis</i>	St Charles Formation	Hellmaria Member	C	Worm Creek Qtzite Mbr	T
<i>Saukiella serotina</i>				C					
<i>Saukiella junia</i>				C					
<i>Saukiella pyrene</i>				C					
Franconian	<i>Ellipsocephaloides</i>	Zonation not established	<i>Proconodontus postero-costatus</i>	Orr Formation	T	T	T		
								<i>Idahoia</i>	T
								<i>Taenicephalus</i>	T
								<i>Elvinia</i>	T

Figure 2.--Correlation of Upper Cambrian and Lower Ordovician strata in the Bear River Range, Utah-Idaho, with those in the southern House Range (Ibex), Utah, and with previous biostratigraphic classifications of Ross (1949) and Hintze (1951). The trilobite zonation follows Winston and Nicholls (1967), Longacre (1970), Stitt (1971, 1977), and Taylor in Hintze and others (1980). Conodont zonation follows Miller (1978, 1980) and Ethington and Clark (1971). Biostratigraphic control for correlations in the Bear River Range column is based on conodonts (C) and trilobites (T).

Cordylodus angulatus Pander s. f., is not appropriate to the Garden City Formation because this form appears only immediately below or within the stratigraphic interval with conodont Fauna C.

The key conodonts composing upper conodont Fauna B are forms not present in the uppermost St. Charles, including Semiacontiodus lowensis (Furnish), "Oistodus" triangularis Furnish s. f., Acanthodus uncinatus Furnish s. f., and multielements "Paltodus" bassleri Furnish, rare "Acanthodus" lineatus (Furnish), and Drepanoistodus(?) n. sp. A. A dominant component of this fauna is represented by striated and nonstriated elements of Utahconus tenuis Miller. Cordylodan form species persist from the upper part of the St. Charles and include developmental variations with secondary basal tips in the lower Garden City Formation ((equals "Cordylodus lindstromi" of Druce and Jones (1971)), Cordylodus angulatus Pander s. f., including C. rotundatus Pander s. f. as an asymmetrical variant, appears in the upper part of upper Fauna B.

Upper conodont Fauna B was recovered from laterally equivalent dolostones and limestones at Hillyard Canyon and Franklin Basin, respectively, and is not strongly lithologically associated in the lower Garden City Formation.

Conodont Fauna C of Ethington and Clark (1971) is recognized in the Garden City Formation at the lowest occurrence of Triangulodus(?) n. sp. A. This species probably descended from Utahconus tenuis and differs primarily by the presence of an oistodiform element (= Oistodus sp. of Ethington and Clark, 1971). Representatives of most of the taxa from the upper part of Fauna B persist into conodont Fauna C of the Garden City Formation. "Acanthodus" lineatus (Furnish) is extremely abundant in Fauna C, while rare specimens of Loxodus bransonii Furnish and common specimens of "Paltodus" spurius Ethington and Clark occur above or at the lowest occurrence of I.(?) n. sp. A at Franklin Basin and Hillyard Canyon, respectively. Protopanderodus asymmetricus (Druce and Jones, 1971), previously described only from the upper Ninmaroo Formation, Queensland, Australia, and Walliserodus n. sp. A are abundant in conodont Fauna C in the Garden City Formation.

Conodont Fauna C appears in abundantly fossiliferous limestones 4.5 m above the base of the Garden City Formation at Franklin Basin and only 0.6 m above the base of the formation at Blacksmith Fork Canyon in crossbedded, linguloid-bearing dolostones. These data support two conclusions: (1) conodont Fauna C is not strongly lithologically controlled in the Garden City Formation and occurs in laterally equivalent dolostones and limestones; and, (2) unless all of upper conodont Fauna B as represented at the Franklin Basin and Hillyard Canyon section is condensed into 0.6 m at Blacksmith Fork Canyon, the base of the Garden City at the latter section is younger than in the northern sections. The second

conclusion provides some information on the relief of the erosional surface developed on the St. Charles Formation prior to deposition of the Garden City Formation in the Bear River Range. The 4.5 m of section with upper conodont Fauna B at Franklin Basin is not present at Blacksmith Fork Canyon. Upper Fauna B is present at least through the lower 11.7 m of the Garden City at Hillyard Canyon. A sub-Garden City Formation erosion surface with approximately 12 m of relief is present in the Bear River Range, Utah-Idaho. The surface is a diachronous unconformity with older units present at the base of the Garden City in the northern sections.

#### PALEOMAGNETISM

Approximately 250 outcrop core samples were collected from the St. Charles and Garden City Formations for analysis of paleomagnetism by S. L. Gillett. Stepwise progressive thermal demagnetization was performed on all samples and a characteristic magnetization was found that has a blocking temperature of less than 500°C.

Preliminary analysis of paleomagnetic data from the St. Charles indicates that the characteristic magnetization is dominantly and perhaps entirely of reversed polarity (declination 179°, inclination -31°), but much scatter is present. In contrast, the Garden City data show normal polarity (declination 357°, inclination 31°) and are more tightly clustered. The directions obtained are not significantly different from being exactly antipodal, and together they yield a preliminary north paleomagnetic pole at 65° N., 74° E. Age of the magnetization is poorly understood. A "fold test" shows the magnetization to be older than Laramide (Cretaceous) folding of the Logan Peak syncline. The low inclination yields a paleolatitude of approximately 17°, a position consistent with independent sedimentological arguments for a low-latitude location for deposition of the St. Charles and Garden City carbonates. The change from reversed to normal polarity occurs at the unconformity between the St. Charles and Garden City Formations, a position within the Early Ordovician Symphysurina Zone. Pervasive remagnetization of the St. Charles and Garden City is contradicted by the opposite polarity between the two formations. We suggest that the reversed-polarity may have been posed on the St. Charles during a relatively short period of diagenesis associated with subaerial exposure prior to Garden City deposition. The duration of the hiatus corresponded to the Hirsutodontus simplex and Clavohamulus hintzei Subzones of the Cordylodus proavus Zone.

Acknowledgments: Ed Landing publishes by permission of the Director, New York State Museum, Science Service, Journal Series number 335. We thank

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## 62. EARLY CAMBRIAN FAUNAS OF EASTERN NEW YORK STATE--TAPHONOMY AND ECOLOGY

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The Early Cambrian fauna known to earlier workers from the Taconic sequence of eastern New York and western Vermont was named the Elliptocephala asaphoides fauna by Lochman (1956, p. 1339), who also discussed its ecology (1956, p. 1348-1349). More recently, the Early Cambrian Acimetopus and Pagetides faunules, as well as Middle and Late Cambrian fossils have been found in the Taconic sequence (Theokritoff, 1964; Rasetti, 1966; 1967; Bird and Rasetti, 1968; Rasetti and Theokritoff, 1967). Theokritoff (1968, p. 18-19; 1979, p. 290-291) interpreted the E. asaphoides, as well as other faunas as shelf-margin or slope faunas, indigenous to that part of the slope situated below the thermocline. He also recognized the possibility that other faunas, such as the Pagetides fauna (Rasetti, 1966, 1967; Rasetti and Theokritoff, 1967) may be upper slope faunas, indigenous to parts of the shelf above the thermocline.

Because much of the carbonate shelf and slope on the eastern margin of North America has been affected by successive orogenies and their associated metamorphism, the distribution of the slope faunas cannot be mapped nor can their bathymetry and relationship to the thermocline be inferred. All that remains is the occurrences in limestones conglomerates, bedded limestones, and shales deposited at the foot of the slope (Bird and Theokritoff, 1967; Rodgers, 1968; Bird and Rasetti, 1968; Keith and Friedman, 1977). An extensive slope may support several habitats, each with its own biota; if so, downslope transport would carry organic remains representative of several habitats into depositional sites on and at the foot of the slope.

### TAXONOMY

In the geological context under discussion, organic remains can be transported in several ways:

#### 1. Settling through the water column.

Vertical transport would affect organisms that live in the water column. Their remains normally would be found in a number of lithofacies, subject to the fossilization potential of the several lithofacies concerned. Depth-stratified organisms probably would show a preference for certain lithofacies.

#### 2. Flows of suspended sedimentary particles and turbidity currents.

The deposits of such flows and currents could enclose organic remains belonging to three categories: (a) organisms indigenous to and initially buried at the site of initial deposition of the sediment, (b) organisms indigenous to sites downslope of the preceding and engulfed and moved downslope, and (c) organisms indigenous to sites of final deposition of the sediment load and buried there.

#### 3. Downslope movement of clasts of consolidated rock.

The consolidation of the sediment takes place at the site of original deposition. Subsequent downslope movement takes place in the form of rock; hence no abrasion, sorting, or incorporation of additional organic remains takes place within the clasts during downslope movement and ultimate deposition.

#### 4. Water currents.

Water currents can pick up, transport, and deposit organic remains and sedimentary particles. These processes may result in abrasion and sorting. Abraded organic remains have not necessarily moved far or even out of their habitat; transportation to and fro may achieve as much abrasion and fragmentation as does transport over significant distances. Water currents can mix remains from distance faunas, as well as separate remains according to size and shape. Concentration of fossils may result from winnowing of sediment and perhaps the more easily moved organic fragments, or from currents sweeping organic remains from a larger area and depositing them in a smaller area.

### THE ELLIPTOCEPHALA ASAPHOIDES FAUNA

The Elliptocephala asaphoides fauna occurs most commonly in clasts of blue-gray saccharoidal limestone within lenses of polymict conglomerate (Lochman, 1956; Theokritoff, 1964; Keith and Friedman, 1977). This blue-gray saccharoidal limestone is not laminated, suggesting that it was not deposited at its site of initial deposition from a sediment flow or turbidity current. Thin sections show some recrystallization of calcite and abundant finely

comminuted organic debris. Faunal lists published by Walcott (1912), Lochman (1956), and Theokritoff (1964) show the consistent and characteristic association within such clasts of Elliptocephala asaphoides, Calodiscus lobatus, Fordaspis nana, Serrodiscus speciosus, Helcionella subrugosa, Hyolithellus micans, Coleoloides prindlei, Hyolithes spp. and inarticulate brachiopods; to these must be added Discinella micans. Although some of the fossils are fragmented, unabraded and unfragmented specimens are abundant, suggesting that the organisms lived in the site of initial limestone deposition. The site of deposition cannot be identified; it may have been on the shelf or on the slope. Of the faunal elements in the limestone clasts, rare fragments of archaeocyaths reported from a few localities in New York by Walcott (1912), Lochman (1956), and Theokritoff (1964) almost certainly were derived from the shelf. Archaeocyathan reefs occur on the shelf in southern Labrador and western Newfoundland, New Jersey, Virginia, and the southern Appalachians (James and Debrenne, 1980). Their absence from the preserved inner parts of the shelf sequence in New York and Vermont suggests that they probably located on the outer part of the shelf here, now obliterated. Yet the paucity and fragmentary nature of archaeocyaths in the conglomerate clasts suggests that there was little significant transport of shelf-derived organic remains onto the slope, with the possible exception of finely comminuted organic debris. Rare examples of Bonnia, Ptychoparella, and Labradoria probably also represent shelf-derived fossils (Lochman 1956, p. 1345-1347); occurrences of Salterella should perhaps be added to this category. Recent work by Lana Spencer (A. R. Palmer, oral communication, 1981) has shown the presence of Calodiscus sp., Discinella micans, Hyolithellus sp., Coleoloides sp. and hyolithids, among other taxa in inter-reef environments on the shelf in southern Labrador (see also James and Debrenne, 1980, p. 1611). I have collected Helcionella sp. from a reef environment in southern Labrador. Although sharing a number of taxa, the southern Labrador shelf and the E. asaphoides faunas are not identical; at least some of the common taxa probably had wider ecological tolerances, and hence more extensive habitats, than others. Additional data are needed from southern Labrador and western Newfoundland to clarify this matter.

The E. asaphoides fauna is less common in laminated bedded limestones deposited by sediment flows (Keith and Friedman, 1977, p. 1229). Whether the organic remains were incorporated in the sediment at the site of initial deposition, or were engulfed during downslope movement, the absence of any forms not associated with the E. asaphoides fauna suggests that that fauna was the lowest fauna with shelled forms on the slope, although it may well have been at

the bottom of that part of the slope receiving carbonate sediment.

The shales have yielded rare E. asaphoides, S. speciosus, and Rimouskia typica (Pasetti, 1967, p. 50, 97; Bird and Rasetti, 1968, p. 28, 31). These species may be individuals carried by currents into sites of mud deposition at the foot of the slope, although they may have had a limited adaptability to areas of mud deposition. On the other hand, Atops trilineatus, known from a number of localities in shales, is rare in limestones (Rasetti, 1967, p. 97), and hence probably is a form adapted to the basin.

#### THE ACIMETOPUS BILOBATUS FAUNULE

The Acimetopus bilobatus faunule was named and described by Rasetti (1966, 1967) from limestone beds at two localities in the Taconic sequence, and from another limestone bed in southern Quebec (Rasetti, 1967, p. 19). Rasetti (1966, p. 2-3) described the occurrence and preservation of the fossils. He considered that the trilobite tests had been subject to transport for considerable time and distance, but he thought that sorting by current action was not entirely adequate to explain the absence of very small eodiscids and large olenellids, inasmuch as very small brachiopods and relatively large eodiscids are common. I suggest that the organic remains may have been sorted in their habitat before being moved downslope with the accumulated sediment. Movement in the sediment flow may have modified the sorting that occurred at the site of initial deposition.

The Acimetopus bilobatus faunule is not the same age as the Elliptocephala asaphoides fauna. Both are found, albeit mutually exclusively, in bedded limestones inferred to have been deposited from sediment flows. Hence, downslope sediment flows carrying the remains of one did not cross the habitat of the other.

#### THE PAGETIDES FAUNA

Several late Early Cambrian faunules from localities in Columbia and Washington Counties, New York, have been subsumed to the Pagetides fauna by Rasetti (1966). They have been listed by Rasetti (1966; 1967, p. 19-20) and Rasetti and Theokritoff (1967, p. 191). At one locality in northern Washington County (Theokritoff, 1964, p. 183, 186, loc. 58-11; Rasetti and Theokritoff, 1967, p. 191), a faunule including agnostid trilobites, Bonnia sp., cf. Lancastria sp., Olenellus sp. (= 'Paedeumias'), Hyolithellus micans, and inarticulate brachiopods was recovered from a boulder of fine-grained dark-gray limestone in a limestone conglomerate lens; thus, the rock enclosing this fauna differs from that enclosing the E.

asaphoides fauna. The trilobites are represented by dissarticulated cephalons, cranidia, and pygidia; thoracic segments are rare. The fossils are sorted into clusters within the rock, and evidently have been carried to their site of burial by water currents. The agnostids were probably carried by currents from the pelagic realm as suggested by Robison (1972, p. 34). Considering the known occurrences and distribution of the remaining trilobite taxa, the remains of most were probably swept from the shelf. Elsewhere in Columbia and Washington Counties, the Pagetides fauna is found in fine-grained dark-gray limestone.

#### CONCLUSIONS

Although additional data are necessary to form conclusions, certain inferences may be advanced tentatively: The Elliptocephala asaphoides fauna was the lowest fauna with shelled forms on the slope. Location below the thermocline best fits the available regional data (Theokritoff, 1979, p. 290-291), but it introduces the apparent anomaly of a calcareous biotope below the thermocline. Calcium carbonate was being deposited on the shelf in an area of high productivity where it is now represented by thick and extensive carbonates. This carbonate could have been carried downslope below the thermocline. If influx were sufficiently fast, saturation would have resulted in the waters abutting the lower slope, facilitating the deposition of carbonate there, particularly at depths above the lysocline. The Acimetopus bilobatus faunule may have occupied a habitat similar to the E. asaphoides fauna. The two were not coeval, supporting Bird and Rasetti's (1968, p. 41) conclusion on stratigraphic order based on other data.

The different rock type enclosing the Pagetides fauna suggests preservation in a different part of the shelf-slope-basin system. The marked role of water currents in the transportation and mixing of the organic remains suggests that the fauna represents a sample from a set of habitats different than the preceding two. However, it does not necessarily follow that this fauna is coeval with one or both of the preceding; the configuration of the shelf and slope may have changed, affecting the sample preserved in the stratigraphic record.

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### 63. MICROFOSSILS FROM THE LOWER CAMBRIAN CAMPITO AND POLETA FORMATIONS, WHITE-INYO MOUNTAINS, CALIFORNIA

By

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The skeletal remains of a new order of Zoantharia (the "septate tubes" of Tynan, 1980) are common elements of microfaunas recovered from acid residues from the Lower Cambrian Campito and Poleta Formations, White-Inyo Mountains, California. The corallites are solitary, and usually cylindrical, although some may be scolecoïd or ceratoid. A thin epithelial layer may be present, and the exterior surface is smooth or annulated. The largest corallites rarely exceed a maximum of 1 mm in diameter, or 5 mm in length. Corallite wall is 0.02-0.05 mm thick and is composed of lamellae of calcium fluoride phosphate  $\text{Ca}_5\text{F}(\text{PO}_4)_3$ ; lamellae dip steeply toward the corallite interior. Longitudinal septa are developed and vary in number (1,2,3,5,7 septa), shape, and continuity. Septal insertion is a process related to ontogeny. Septal insertion pattern is bilateral and cyclic, as in scleractinian corals. Through all growth stages, the corallite lacks (1) an analogue to the countercardinal septum, (2) pores, (3) any axial structures, (4) tabulae, (5) dissepiments, and (6) septal grooves. These corallites constitute the oldest occurrence of "stoney corals" reported from southwestern United States. They occur within archaeocyathid-bearing carbonate units in association with trilobites, helcionellids, hyolithids, hyolithellminthids, foraminifers, chancellorid sponges, edrioasteroids, eocrinoids (heliocoplacoids? and possibly 2 additional echinoderm classes), "ostracodes" and other crustaceans, inarticulate brachiopods, several mitral-shaped (tommotid-like) forms, and other problematical microfossils. These fossil assemblages are within the Lower Cambrian (Atdabanian) Nevadella Zone.

Poorly preserved, laterally compressed hat-shaped skeletal remains (monoplacophorans?) have been recovered from acid residues of the upper member of the Deep Spring Formation. These fossils occur well below the lowest trilobites of the Lower Cambrian sequence in eastern California, and seem to indicate a possible Tommotian Age for the unit.

It is essential that the faunal succession of this and other poorly known Lower Cambrian sequences be studied in detail, described, and documented. Such studies will provide paleobiologists with (1) important data for analysis of diversity trends in the Phanerozoic, (2) a better understanding of Early Cambrian faunal provinces and provincialism, (3) critical information required to evaluate hypotheses concerning the origin of major invertebrate groups, and (4) a reliable data base from which to judge the character and geological significance of the "Cambrian radiation event". Similar micropaleontological investigations may lead to a more satisfactory resolution of the Precambrian-Cambrian boundary problem.

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## 64. MICROPALAEONTOLOGY AND BIOSTRATIGRAPHY OF THE LOWER CAMBRIAN SEQUENCE IN SCANDINAVIA

By

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This report summarizes published (Vidal, 1981b) and unpublished micropaleontologic data from Lower Cambrian rocks in Denmark (the Island of Bornholm), Sweden (Scania, the Kalmar Coars, ~~Västergötland~~, Vassbo, Laisvall, Torneträsk) and southern Norway (the Lake Mjøsa district). Stratigraphic sequences in these areas consist of basal Cambrian quartzitic units that are barren or extremely sparsely fossiliferous and traditionally referred to the Platysolenites antiquissimus and Mobergella holsti Zones (see further, Martinson, 1974; Ahlberg and Bergström, 1978). Succeeding arenaceous and (or) argillaceous units have yielded occasional trilobites, brachiopods, and hyolithids, which in general terms are assigned to the Holmia Zone.

Acritarch zones have not been defined as yet for the Lower Cambrian. However, their stratigraphic distribution in the Lower Cambrian sequences of the Russian Platform and Poland are sufficiently well known to allow detailed correlation (Volkova and others, 1979). Thus, distinctive assemblages of acritarchs characterize the local units established in the Russian Platform (that is, Rovno, Lontova, Lükati, Vergale and Rausve Beds; fig. 1). The same condition is also true of the Polish Lower Cambrian, which is subdivided into a lowermost Cambrian Klimontov Stage (sometimes called Sub-Holmia "horizon", alternatively "zone", embracing the Sabellidites, Platysolenites, and Mobergella Zones), Holmia Zone, and Protolenus Zone. The Klimontov Stage (Sub-Holmia) is thus correlated with the Rovno and Lontova Beds of the Russian Platform. The Holmia Zone is correlated with the Lükati and Vergale Beds, and the Protolenus Zone with the Rausve Beds of the Russian Platform.

In this paper, the terms sub-Holmia "stage" and Holmia "stage" are used with an extremely informal meaning. I have done so only for practical reasons, because in my opinion, this provides the simplest way of setting the present material in relation to rock units and time-stratigraphic units defined for the Russian Platform and Poland that are regarded by Russian and Polish workers as time-equivalent (see further, Volkova and others, 1979).

With the exception of basal quartzitic units in southeastern Scania (the Lunkaberg and Vik Sandstones; figs. 1, 2) and in southern Norway (the Vangsås Formation; fig. 2), which are micropalaeontologically barren (Vidal, 1981b), all these fossiliferous and unfossiliferous units have yielded acritarch assemblages indicating Holmia A and B ages (Vidal 1981b; see fig. 1). Thus, acritarchs diagnostic of Holmia age have been recovered from rock units in the Mjøsa district that have yielded P. antiquissimus and Mobergella. Further, Mobergella-bearing rocks at the Kalmar Coast area also yielded acritarchs indicative of a Holmia age (fig. 1), which are comparable to acritarchs from the Mobergella Zone in Poland (Moczydlowska, oral commun. 1980). The Mobergella fauna was regarded by Bengtson (1970) as contemporaneous with the uppermost Tommotian Stage of the Siberian Platform. If this correlation is correct, then the upper Tommotian perhaps could be correlated with the Holmia Zone of the Russian Platform, Poland and Scandinavia.

Acritarch evidence is here interpreted as indicating that the sub-Holmia "stage" may not be represented in Scandinavia (figs. 1, 2). Thus, the Early Cambrian transgression(s) reached Scandinavia in Holmia A time; the Holmia B transgression being the most comprehensive. In the cratonic shield areas, rocks of Holmia age rest on Precambrian crystalline rock complexes with profound unconformity. However, in the eastern margin zone of the Caledonian fold belt, the same strata rest either on uppermost Proterozoic (Vendian) sedimentary rocks (for example, in the Mjøsa district, at Laisvall and at Torneträsk; Vidal 1981a, see fig. 2) or on much older Proterozoic rocks (for example, at Vassbo).

The ages and correlations indicated by micropalaeontological evidence have a number of implications. Thus, the stratigraphic range of P. antiquissimus (as further indicated by macropalaeontological evidence; see further Bergström, this volume) is considerable. Furthermore, the implication of correlations based on this and

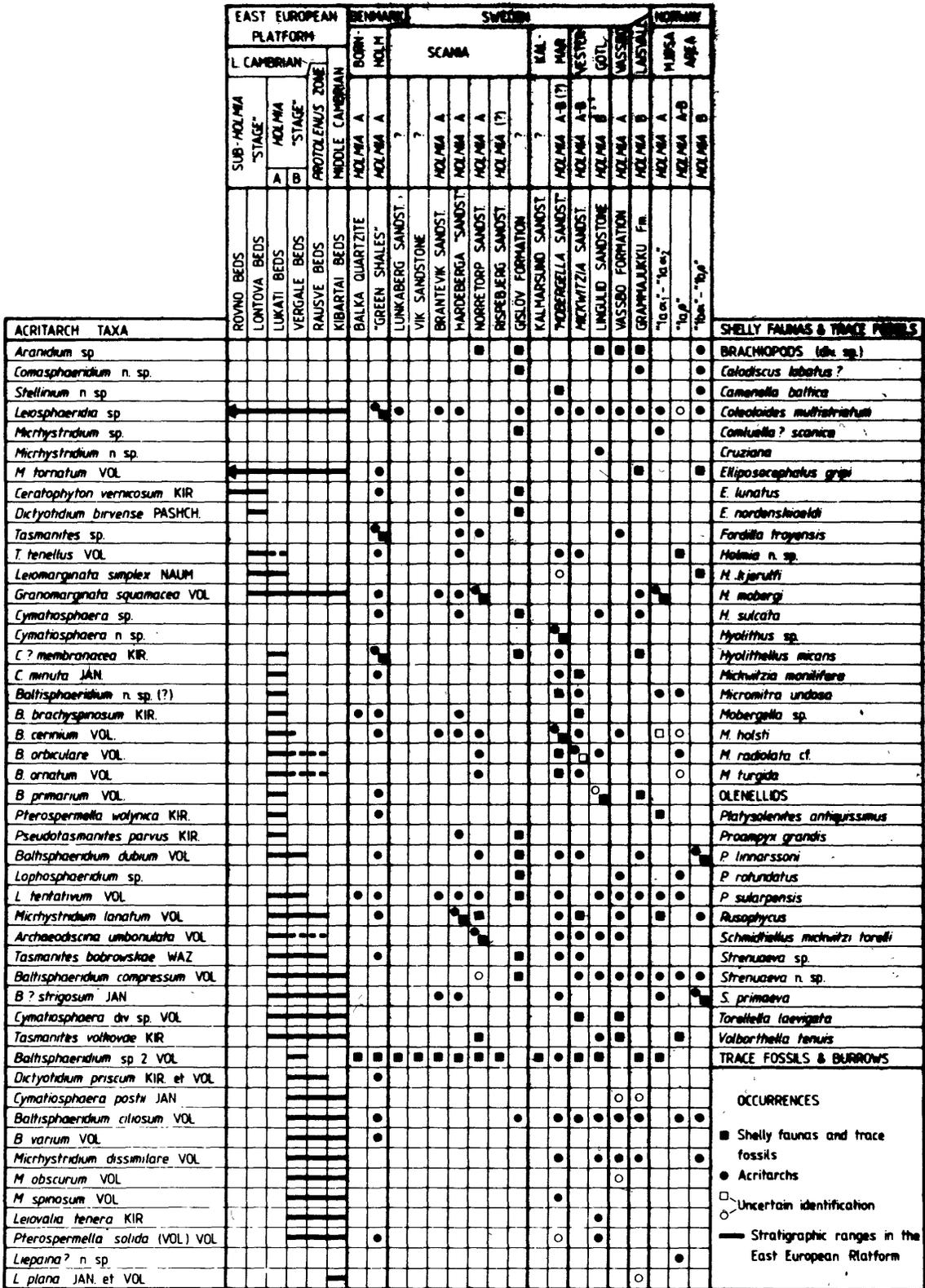


Figure 1.--Stratigraphic distribution of acritarchs in the Lower Cambrian of the Russian Platform, Poland (modified from Volkova and others, 1979) and Scandinavia, and distribution of shelly faunas and trace fossils in Scandinavia (modified from Martinsson, 1974; Bergström and Ahlberg, 1981).

STRAT	ZONATION		DENMARK		SWEDEN		S. NORWAY		SWEDEN		
	Trilobites	Shells	(Bornholm)	Scania	Kalmar	Västergötland	Mjøsa	Vassbo	Laisvall	Torneträsk	
CAMBRIAN	A-B Holmia	PROAMPYX, HOLMIA KJERULFI		GISLÖV Fm. SHALE & LIMESTONE		LINGULID SANDSTONE	"1b $\alpha$ " - "1b $\beta$ " SHALE		GRAMMAJUKKU Fm	UPPER SHALE Fm	
		HOLMIA n sp	VOLBORTHELLA TENUS	RISPEBERG SANDSTONE	RISPEBERG SANDSTONE		"1a $\beta$ " SILTSTONE			UPPER SANDSTONE Fm	
	Sub-Holmia (?) Holmia A	SCHMIDTIELLUS, HOLMIA	VOLBORTHELLA, PLATYSOLENITES, MOBERGELLA	"GREEN SHALE" (GRÖNNE SKIFRE)	NORRETORP SANDSTONE	"MOBERGELLA"	HICKWITZIA SANDSTONE	"1a $\alpha_1$ - 1a $\alpha_2$ " SANDSTONE, SILTSTONE	VASSBO Fm		MIDDLE SHALE Fm
		RUSOPHYCUS PARALLELUM	BALKA QUARTZITE & NEXÖ SANDSTONE	HARDEBERGA QUARTZITE	BRANTEVIK SANDSTONE & VIK SANDSTONE	SANDSTONE & KALMARSUND SANDSTONE		WINGSÅS Fm (RINGSÅKER QUARTZITE & VARDAL SANDSTONE MEMBERS)			
VENDIAN PRE-CAMBRIAN			LUNKABERG SANDSTONE			VEDMARK GROUP (VENDIAN)		SÄVVÖVARE & ACKERSELET FORMATIONS		SANDSTONE & SHALE	

Figure 2.--Suggested correlation of the Scandinavian Lower Cambrian. Zonation modified from Bergström and Ahlberg (1981; see further, Bergström, 1981, this volume). A indicates acritarch occurrences.

related fossils in northern Scandinavia (see further, Fåyn & Glaessner, 1979) is that rocks of the Dividal Group containing *P. antiquissimus* may in fact be of *Holmia* age. This derives indirectly from accepting the correlations proposed by Fåyn & Glaessner (1979) between the Mjøsa area (southern Norway) and northern Scandinavia. However, the presence of *Sabellidites cambriensis* (if correctly identified) and *Aldanella kunda* in rocks of the Dividal Group (see further, Fåyn & Glaessner 1979) would suggest the existence of rocks attributable to the sub-*Holmia* "stage" (Rovno and Lontova Beds, respectively). However, the long stratigraphic range presently established for *P. antiquissimus* should be taken as a signal for caution in interpreting the stratigraphic significance (for more than generalized correlation purposes) of these fossils. It may well be so that the above fossils have in Scandinavia stratigraphic ranges comparable to that of *P. antiquissimus*. An indication in that direction is provided by the admittedly rather circumstantial evidence presented by the occurrence of *Rusophycus* in the lower Breivik Formation (partially equivalent to the Dividal Group; see further, Fåyn and Glaessner, 1979) in Finnmark, stratigraphically well below an occurrence of *P. antiquissimus*. No reliable micropalaeontological data are as yet available from the Breivik Formation (see further, Vidal 1981a), but records of *Rusophycus* elsewhere (in Scania and in the Mjøsa area) have invariably proved to be of *Holmia* age (fig. 1).

Also deriving from the above is the fact that correlation between the Scandinavian and Baltic Lower Cambrian sequences, on the one hand, and the Tommotian of the Siberian Platform, on the other, must be regarded as extremely tentative and perhaps open to future revision.

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## 65. CAMBRIAN ROCKS OF THE ELLSWORTH MOUNTAINS, WEST ANTARCTICA

By

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The Ellsworth Mountains of West Antarctica (fig. 1) are the highest mountains in Antarctica, reaching elevations of 5120 m. They are divided into a northern range, the Sentinel, and a southern range, the Heritage. Reconnaissance geologic mapping conducted during four expeditions from 1962 to 1975 have established the existence of extensive Middle and Upper Cambrian rocks within a stratigraphic sequence of about 13,000 m (Craddock, 1969; Craddock and others, 1964; Hjelle and other, 1978). During the 1979-80 austral season, a group of 42 scientists (principally geologists) conducted detailed geologic studies in the Ellsworth Mountains (Spletstoeser and Webers, 1981). Although many of the investigations of the rocks, fossils, and field data from the latter expedition are still in a preliminary stage, a general picture of the Cambrian rocks of the Ellsworth Mountains can be outlined.

Almost all Cambrian rocks of the Ellsworth Mountains are exposed in the Heritage Range where they make up about 50 percent of the exposed bedrock. The recovery of seven or more Middle and Upper Cambrian trilobite faunas has permitted assignment of at least 2900 m of strata to those series (fig. 2). The lower 7800 m of the stratigraphic column probably was deposited during the Cambrian.

Cambrian rocks are found in the Heritage Group, the Minaret Formation, and the lower part of the Crashsite Quartzite. The strata are characterized by rapid facies changes. The lower 3050 m of Heritage Group strata are volcano-clastic and are considered to consist primarily of ash-flow tuffs and (or) lahar deposits. A thick polymictic conglomerate occurs near the base of the unit. Above 3050 m is a series of graywackes, conglomerates, quartzites, black slates, marble units, and interbedded volcanics. The sedimentary rocks are considered to represent deposition in fluvial, deltaic, and shallow marine environments. The Upper Cambrian Minaret Formation, previously considered to be at the base of the stratigraphic column (Craddock, 1969) overlies the Heritage Group. It is primarily marble with minor interbeds of black slate and argillite. It is thickest in the southern Heritage Range, and is thin or absent in the northern Heritage. It is considered to be a normal marine deposit in which trilobites are found at a number of localities. The fauna (Webers, 1972) also

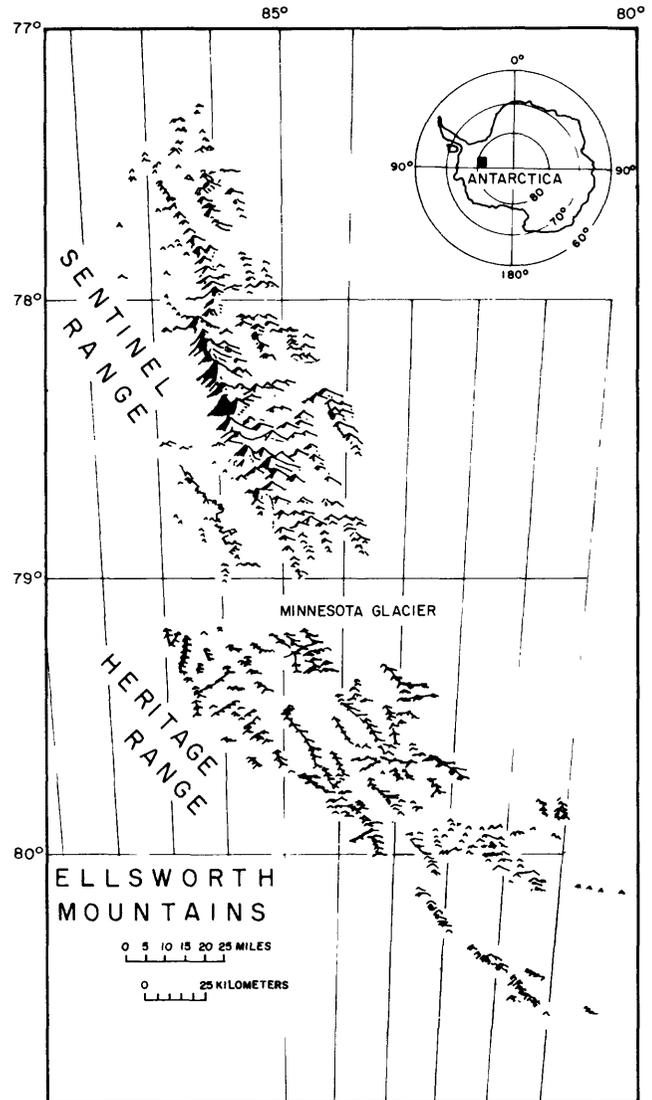


Figure 1.--Generalized physiographic map of the Ellsworth Mountains with inset of Antarctica.

includes articulate and inarticulate brachiopods, pelmatozoans, archaeocyathids, rostroconchs, hyolithids, algal structures, and a variety of monoplacophorans. An unknown thickness of the lower Crashsite Formation contains Upper Cambrian strata.

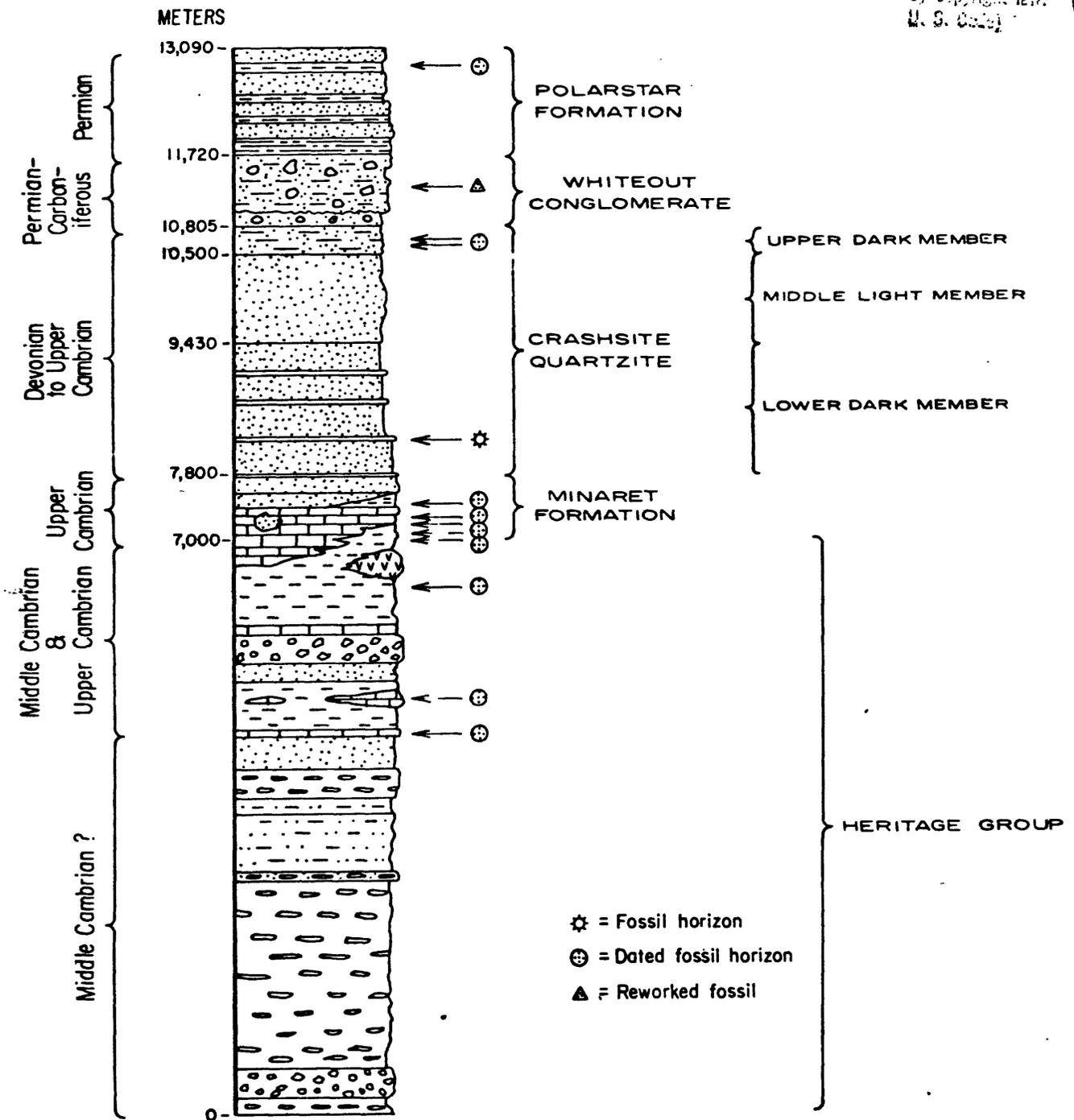


Figure 2.--Preliminary columnar section for Middle Cambrian (?) through Permian strata in the Ellsworth Mountains, Antarctica.

Paleontologic interpretations supported by paleomagnetic evidence indicate a tropical latitude for the Ellsworth Mountains in the Late Cambrian.

This report is preliminary: All fossil faunas, the field data, and all rocks collected during the 1979-80 season and some of the previous seasons are under active study.

The writer thanks the National Science Foundation and the U.S. Navy for extensive financial and logistic support (Grant DPP 7821720 to Macalester College, G. F. Webers, Principal Investigator). John Spletstoesser critically read the manuscript.

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## 66. THE BURGESS SHALE FAUNA AND THE EARLY EVOLUTION OF METAZOAN ANIMALS

By

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The fauna of the Burgess Shale includes species of animals that had mineralized hard parts, such as brachiopods, monoplacophoran molluscs, hyolithids, echinoderms and trilobites, but two-thirds of the 150 species were soft-bodied. In the marine realms surrounding the North American and other continents the hard parts of different Cambrian faunas are known. If these species with hard parts were accompanied also by twice as many kinds of so far unknown soft-bodied animals, Cambrian faunas were far more diverse than presently recognized. The Burgess Shale fauna is dominated by arthropods, predominantly soft-bodied; rarely are there two species of one genus, and morphological gaps at family or higher taxonomic level separate the type species. The latter is also true of the varied and highly abundant worms, and the rare echinoderms. No species is interpreted as showing characters intermediate between two phyla. Nineteen percent of the genera cannot be placed in any Holocene phylum; on the other hand certain species show characters typical of major younger groups, such as crustaceans, crinoids, and chordates. In the Early Cambrian, three different groups of trilobites are present, and because almost nothing is known of their soft parts, their relationships are uncertain. Attention has recently been drawn to the heterogeneity of Early Cambrian brachiopods, and species of echinoderms have been described from Cambrian rocks of widely separated geographical areas. The Cambrian pattern of evolution thus shows many discrete, parallel lines of descent, and the abundant hard-shelled animals are not those that dominate the marine life of later periods. Few soft-bodied animals of uncertain affinities are known from rocks younger than the Burgess Shale.

Soft-bodied Cambrian metazoans, therefore, may have been abundant and varied, at the same time as hard-shelled forms were beginning to appear and diversify. The morphological discontinuities between

kinds, and the number of strange forms, may be a reflection of less strong competition during the early occupation of marine environments. In the succeeding Ordovician Period, hard-shelled groups, little represented earlier, underwent spectacular adaptive radiations--the cnidarians, molluscs, articulate brachiopods, bryozoans, and echinoderms. A concomitant may have been the extinctions of many of the strange Cambrian animals, and another was the beginnings of the dominance of particular groups that constitute our Holocene phyla.

What little is known of Cambrian geography suggests the existence of a large Gondwanaland continent and several smaller land areas, each surrounded by shallow seas. These shelf areas were separated by oceans of uncertain width and depth, that may have acted as partial barriers to migration. Thus, evolution may have proceeded independently in different areas at particular times, giving rise to widely different lines of descent. Possible geographical factors in evolution cannot be discounted, but the distribution in time and space of Cambrian animals is too poorly known to allow assessment of them.

Precambrian metazoan faunas offer little clue to the origins of Cambrian animals, but the pattern of Precambrian evolution may have been as complex as that of the Phanerozoic, representing varying rates, extinctions, geographical isolation and dispersal. The many distinct lines of descent that are recognizable in the Early Cambrian are the product of this pattern, which was generated over an unknown length of time, in a world so far hidden from us. A common theory is that metazoan animals diverged from a single origin, but an equally plausible theory is that they arose more than once. Particular grades of organization, such as the brachiopod, or arthropod, or echinoderm grade, may each have arisen more than once along separate lines of descent.

## 67. CLASSIFICATION AND CORRELATION OF THE CAMBRIAN SYSTEM IN CHINA

By

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The Cambrian System in China is well developed, and includes various types of sedimentation and a variety of biotas. According to the results of many years of research, the system may be divided into three series and ten stages: the Lower Cambrian Series composed of the Meishucunian, Qiongzhusian, Canglangpuan, and Longwangmiaoan Stages; the Middle Cambrian Series, composed of the Maozhuangian, Xuzhuangian, and Zhangxian Stages; and the Upper Cambrian Series, composed of the Kushanian, Changshanian, and Fengshanian Stages.

1. The Meishucunian Stage yields the oldest shelly faunas and is the lowest stage of the Cambrian System in China. Its faunas include Hyolitha, Hyolithelmites, Brachiopoda, Gastropoda, Monoplacophora, Rostroconchia, Porifera, etc., but no trilobites. On the basis of preliminary works it is divisible into two faunal assemblages: a lower, Anabarites-Circotheca assemblage, represented mainly by primitive and simple fossils such as Anabarites, Circotheca, Turcotheca, and Protohertzina; and an upper Allatheca-Yunnanotheca assemblage, comprising various kinds of small fossils such as Allatheca, Quadrotheca, Lophotheca, Yunnanotheca, Tiksitheca, Hyolithellus, Torellia, Siphogonuchites, Sachites, Latouchella, Pelagiella, Heraultipegma and Chancelloria.

2. The Qiongzhusian Stage is divisible into two parts. Its lower part includes a part of the nontrilobite zone and contains Turcotheca, Hyolithellus, Scenella, Obolus, Chancelloria, and Plagiogmus. Owing to insufficient research, the fossil zones or assemblages are not yet named. The upper part is characterized by the occurrence of the ancient trilobites Parabadiella, Eoredlichia, and Wutingaspis, which form the Eoredlichia Zone. Bradolina are very common, while the primitive archaeocyathids Ajacicyathus and Taylorcyathus first appear here. There is also a great change in the composition of Hyolitha. In the micropaleoflora, Micrhystridium and Baltisphaeridium, predominate.

3. The Canglangpuan Stage is characterized by the absence of ancient trilobites such as Parabadiella and Eoredlichia and by the presence of particular Drepanopygidae and Gigantopygidae. It also was a flourishing age in the development of trilobites such as

the Ellipsocephalidae, Mayiellidae, Protolenidae, and Dorypygidae. This stage contains three zones: in ascending order, the Yiliangella-Yunnanaspis, Drepanuroides, and Palaeolenus Zones. It is also the level with the most diverse development of Archaeocyatha in China.

4. The Longwangmiaoan Stage is characterized by the disappearance of Drepanopygidae, Gigantopygidae, Mayiellidae, and Dolerolenidae and by the appearance of various species of Redlichia, which are characterized by having their anterior facial sutures strongly directed laterally. Only one fossil zone, the Hoffetella-Redlichia murakamii Zone, is established.

5. The Maozhuangian Stage is characterized by replacement of the redlichids by ptychopariid, chittidillid, and agraulid trilobites such as Shantungaspis, Psilostracus, Probowmania, Kunmingella, Chittidilla, Plesiograulos, and Paraagraulos. One zone, the Shantungaspis Zone, is established.

6. The Xuzhuangian Stage is marked by a sharp increase in trilobites. Besides the agnostids, there are many forms of the Dorypygidae, Dolichometopidae, Corynexochidae, Ptychopariidae, Alokistocariidae, Conocoryphidae, Solenopleuridae, Agraulidae, Anomocaridae, Proasaphiscidae, and Anomocarellidae. The stage contains four zones in ascending order: the Kochaspis, Sunaspis, Portiagraulos, and Bailiella Zones.

7. The Zhangxian Stage shows a maximum development in the number of the trilobite taxa. It is divided into three zones in ascending order: the Crepicephalina, Amphoton-Taitzula, and Damesella Zones.

8. The Kushanian Stage contains a very peculiar fauna. On the one hand, damesellids typical of the Zhangxian Stage continued to develop, such as Blackwelderia, Stephanocare, Drepanura, Bergeronites and Dorypygella, whereas, on the other hand, there were the special endemic genera Liostracina, Shantungia, and Diceratocephalus as well as cosmopolitan agnostids such as Glyptagnostus, Homagnostus, and Pseudagnostus. The stage is divided into two zones: in ascending order, the Blackwelderia and Drepanura Zones.

The Kushanian is also an important age for the development of conodonts, including Furnishina, Prosaqittodontus, Prooneotodus, Hertzina, Westergaardodina, and Proacodus. One conodont zone, the Westergaardodina matsushitai Zone, is established.

9. The Changshanian Stage is characterized by a marked decline in Damesellidae and the appearance of forms belonging to the Kaolishaniidae, Changshaniidae, Leostegiidae, Komaspidae, and Elviniidae. It is divided into three trilobite zones: in ascending order, the Chuangia, Changshania, and Kaolishania Zones. A conodont zone, the Distacodus? palmeri Zone, is also recognized. In recent years such graptolites as Dendrograptus, Callograptus, and Dictyonema have been found in the Chuangia zone at Xiaoshan of Anhui, marking the lowest graptolite horizon for North China.

10. The Fengshanian Stage is marked by such families as the Ptychaspiidae, Saukiidae, and Tsinaniidae. It is divided into three zones: in ascending order, the Ptychaspis-Tsinania, Quadraticephalus-Dictyella, and Calvinella-Mictosaukia Zones. Conodonts are very abundant. Two conodont zones, Proconodontus rotundus and Corylodus proavus, have been established. The former is equivalent to the Ptychaspis-Tsinania and Quadraticephalus-Dictyella Zones, while the latter is equivalent to the Calvinella-Mictosaukia Zone.

The cephalopod fauna of the Fengshanian Stage is significant in that it is probably the earliest one in the world. The Ptychaspis-Tsinania zone contains Plectronoceras, whereas the middle and upper parts of the Fengshanian yield Paraplectronoceras, Ellesmeroceras, Eoclarkoceras, Protoactinoceras, Sinoeremoceras, and Wanwanoceras.

Within the Middle and Upper Cambrian, two biofacies complexes can be recognized: the North China and the Jiangnan biofacies. The faunas of the North China biofacies include all of the trilobite zones mentioned above, whereas the faunas of the Jiangnan biofacies, which are mainly planktonic trilobites, small inarticulate brachiopods, and sponge spicules, are distributed in the Tianshan Mountains and Kuruktag of Xinjiang, the Baishan Mountains of Gansu, Hunan, Western Zhejiang, South Anhui, and Hainan Island of Guangdong. According to preliminary research by the author and T. R. Zhang, the Middle Cambrian comprises, in ascending order, the Xystridura Zone, the Ptychagnostus atavus Zone, the Ptychagnostus punctuosus-Goniagnostus nathorsti Zone, and the Lejopyge laevigata Zone; the Upper Cambrian is divided into the Clavagnostus-Homagnostus Zone, the Glyptagnostus stolidotus Zone, the Glyptagnostus reticulatus Zone, the Xestagnostus Zone, the

Lotagnostus punctatus-Hedinaspis Zone, and the Lotagnostus hedini Zone. As for the correlation between the two biofacies complexes, it is worth noting that representatives of Ptychagnostus occur in the Bailiella Zone of the Xuchuangian and that Ptychagnostus atavus is associated with Crepicephalina in Xinjiang; hence the Ptychagnostus atavus Zone may approximately correspond with the Bailiella and Crepicephalina Zones. Furthermore, as the Ptychagnostus punctuosus-Goniagnostus nathorsti Zone contains many elements of Amphoton, Sunia, and Fuchouia, it is certainly equivalent to the Amphoton-Taitzuia Zone, and consequently the Lejopyge laevigata Zone must correspond to the Damesella Zone. The associations of Glyptagnostus stolidotus with Bergeronites, Dorypygella, and Liostracina; of Glyptagnostus reticulatus with Chuangia; and of Changshania with Irvingella are significant evidence for the correlation of fossil zones within China and abroad.

The Eoredlichia Zone in China is directly equivalent to the same in Australia, and its lower boundary may approximately correspond with the base of the Atdabanian Stage of the U.S.S.R. and the base of the Fallotaspis Zone in North America and Morocco. As the genus Kochaspis occurs in the upper part of the Plagiura-Poliella Zone in North America, the latter may be correlated with the Kochaspis and Shantungaspis Zones. Zones of the Jiangnan biofacies of the Middle Cambrian are equivalent to the Xystridura, Ptychagnostus gibbus, P. atavus, Hypagnostus parvifrons, P. punctuosus, Goniagnostus nathorsti, and Lejopyge laevigata Zones in Queensland, Australia, but some zonal fossils are mixed in China, therefore only four zones can be recognized here. In the Upper Cambrian, there are cosmopolitan trilobite genera and species, and thus the correlations are more reliable. The Kushanian Stage may be approximately correlated with the Mindyallan Stage of Australia. If the Mindyallan includes the Erediaspis erectes and Damesella toyosa-Ascionepea janitrix Zones, the base of the Mindyallan is a bit lower than that of the Kushanian. The coexistence of Chuangia, Aphelaspis and Glyptagnostus reticulatus shows these zones may be equivalent among themselves. The Changshania Zone, which yields Irvingella, may be compared to the Elvinia Zone of the U.S.A. The Taenicephalus and Saratogia Zones assigned to the Ptychaspid Biome should be correlated with the Ptychaspis-Tsinanian and Quadraticephalus-Dictyella Zones. The Calvinella-Mictosaukia Zone of the Fengshanian Stage in China approximately coincides with the Mictosaukia perplexa Zone of the Payntonian Stage of Australia and with the Saukia Zone of the Trempealeuan Stage of the U.S.A.

## 68. THE CAMBRIAN-ORDOVICIAN BOUNDARY IN CHINA

By

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The transition from the Cambrian System to the Ordovician System occurred during a geotectonically quiet stage in China, so that many fine continuous sequences were deposited. The Cambrian-Ordovician boundary may be differentiated in three types of stratigraphic sequences based on biofacies and lithofacies characteristics.

The first type is a flysch sequence composed mainly of rhythmic shales and sandstones, which formed within a miogeosyncline (for example, the graptolitic facies of southeast China). The boundary may be represented in the Taishan section of Guangdong. Fossils above the boundary are Pacific-type graptolites, while those below it are mostly inarticulate brachiopods. The Lower Ordovician Xinchang Formation contains, in ascending order, the Staurograptus-Anisograptus Zone, the Aletograptus-Triograptus Zone and the Adelograptus-Clonograptus Zone. At present the base of the Staurograptus-Anisograptus Zone is tentatively regarded as the Cambrian-Ordovician boundary. This boundary type is similar to that of Victoria, Australia, and western North America.

The second facies type is a carbonate rock sequence consisting of limestones and dolomites, which developed on the platform and which contains, with mainly shelly facies biota, as shown by the sequences in Tangshan of Hebei (north China region), Yichang of Hubei (Yangzi region), and Ulan of Qinghai (Qaidam region).

Previously the Cambrian-Ordovician boundary was recognized between the highest trilobite zone of the Upper Cambrian in Tangshan, that is, between the Mictosaukia-Calvinella Zone and the Lower Ordovician Asaphellus trinodus Zone. However, Z. Y. Zhou and J. L. Zhang (1978) discovered and named the Leiostridium (Euleiostridium)-Aristokainella and the Onychopyge-Leiostridium (Alloleiostridium) assemblages below the Asaphellus trinodus Zone. According to research on conodonts by T. X. An (unpubl.), the Ordovician boundary is marked by the Cordylodus proavus Zone, which corresponds to the Mictosaukia-Calvinella Zone. Above the Cordylodus proavus Zone are, successively, the Drepanodus simplex (Monocostodus seviervensis) Zone and the Cordylodus rotundus-"Acodus" oneotensis Zone, which are equivalent to the Onychopyge-Leiostridium

(Alloleiostridium) and the Leiostridium (Euleiostridium)-Aristokainella assemblages respectively.

The Cambrian-Ordovician boundary was previously drawn at the base of the Nanjinguan Formation in Yichang of Hubei, namely at the base of the Asaphellus inflatus Zone. Below this zone was later discovered Dictyonema flabelliforme yichangense. Recently, Drepanodus simplex was found within the top 10 m of the underlying Sanyoudong Group, which was formerly assigned to the Upper Cambrian, and Cordylodus proavus and Proconodontus notchpeakensis were obtained from the bed situated about 20 m below the top of the Sanyoudong Group. These new findings indicate that the Cambrian-Ordovician boundary should be placed at the horizon approximately 10 m below the top of the Sanyoudong Group.

The Walcottoceras-Dakeoceras cephalopod assemblage recently discovered in Ulan, Qinghai Province, may be correlated with the Lower Ordovician Gasconadian Stage of North America. The Cambrian-Ordovician boundary is drawn below this assemblage.

In general, this boundary is similar to that of carbonate platform sequences in Utah and Oklahoma, U.S.A., and in Queensland, Australia. In China the boundary is drawn between the Mictosaukia-Calvinella and Onychopyge trilobite zones, or between the Cordylodus proavus and Drepanodus simplex conodont zones. This boundary may be equivalent to that between the Saukia Zone of the Trempealeau Stage and the Missisquoiia Zone of the Canadian Series in the U.S.A.; and between the Mictosaukia perplexa Zone of the Payntonian Stage and Datsonian Stage in Australia.

A similar trilobite fauna occurs in Baoshan of western Yunnan, but in clastic rocks. The highest zone of the Upper Cambrian Baoshan Formation, the Mictosaukia-Calvinella Zone, is overlain by the Lower Ordovician graptolite Dictyonema flabelliforme liaotungense. According to the sequence in Liaoning, this graptolite does not represent the lowest graptolite zone of the Ordovician. In Thailand, the Tarutao Sandstone contains Mictosaukia, Coreanocephalus Pogodia, and Saukiella, which may be correlated with the Mictosaukia-Calvinella Zone. The Cambrian-Ordovician boundary is drawn between these trilobites and the fossil beds with asaphoid trilobites.

The third type of boundary sequence consists of siliceous limestones and mudstones or nodular limestones deposited at the carbonate platform margin, which contains a biota of shelly or mixed facies. For example, in Huocheng of Xinjiang, Badin Jaran of Nei Mongol, Changshan of Zhejiang, Wuning of Jiangxi, and Taojiang of Hunan.

The uppermost part of the Upper Cambrian in Huocheng contains Lotagnostus, Diceratopyge, and Hedinaspis, whereas the lowest part of the Lower Ordovician yields Hysterolenus, Rhadinopleura, and Niobella. The distance between these fossil horizons is less than 2 meters. The boundary is also placed between the Hedinaspis-Diceratopyge assemblage and the Hysterolenus assemblage in Badin Jaran. The boundary in these two regions correlates with that of Kazakhstan, U.S.S.R., and the boundary between the Hedinaspis sculcata bed and the Rhadinopleura piriforme bed in the U.S.S.R.

The Cambrian-Ordovician boundary in Changshan of Zhejiang and Wuning of Jiangxi is fixed between the Lotagnostus hedini Zone and the Hysterolenus Zone. In

Taojiang of Hunan the Upper Cambrian contains Lotagnostus, Hedinaspis, and Charchaia, while the Lower Ordovician yields Dictyonema flabelliforme sociale and Staurogaptus diffusus. The Cambrian-Ordovician boundary in these regions is similar to that of Sweden, where it is placed between the Dictyonema shales and the Olenid shales. The lowest zone, the Dictyonema flabelliforme dimograptoides Zone in the Dictyonema shale, includes Hysterolenus and may approximately correspond with the Hysterolenus Zone in China.

In China, it seems most suitable to recognize the Cambrian-Ordovician boundary at the boundary between the Hysterolenus and Lotagnostus hedini Zones (or at the Lotagnostus-Hedinaspis assemblage), between the Onychopyge and Mictosaukia-Calvinella zones, and between the Drepanodus simplex and Cordylodus proavus Zones. These horizons correspond to the base of the Tremadocian Series and also coincide with the placement of the Cambrian-Ordovician boundary by scientists in most other countries of the world.

## 69. A SURVEY OF SALTERELLA (PHYLUM AGMATA)

By

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The Early Cambrian species of Salterella have been variously classified since the genus was first described by Billings (1861). As currently known, the genus has neither precursors nor descendants. Most recently the genus was assigned as the sole member of the extinct phylum Agmata (Yochelson, 1977), and its biologic placement has not been discussed further. The genus has no obvious relationship to any other group of phylum rank.

### GENERAL MORPHOLOGY

Examination of specimens from areas not previously studied confirms the details of morphology given earlier (Yochelson, 1977). Individuals consist of a small calcareous-walled narrow cone, approximately the size and shape of the lead in a pencil point. In this cone, exceedingly fine-grained clastic particles form layers, each lamina presumably having been cemented in place by a sheet of calcium carbonate (Griffin and Yochelson, 1975). As the cone grew larger more laminae were emplaced. A central tube is present though all the laminae. During life the tube was probably occupied by a strand of tissue that maintained contact with the apex of the cone. The organism apparently was not concerned with the mineralogy of grains used to form the laminae, but only with the size of the grain. Composition of the Salterella cones vary widely among localities, depending on what grains were available to the animal.

Because specimens are small, they were readily subject to movement by weak waves and currents. Often individuals are aligned or concentrated in the troughs of ripples. Most are broken at the aperture and many at the apex. Poorly preserved material is many times more common than good specimens. As a further complication, the shell may be partially penetrated by crystal growth in the matrix or partially dissolved. Where specimens are filled predominantly with siliceous grains, they commonly weather in relief; where filled with calcareous material, they usually do not. In a few localities, the shell is silicified, but these occurrences are exceptional.

### STRATIGRAPHIC RANGE

Salterella is known through only part of the Bonnia-Olenellus Zone and is thus an excellent indicator of a late part of Early Cambrian (Yochelson, 1977); no more precise date can yet be given.

Detailed collecting of local sections indicates that Salterella is quite restricted vertically. For example, Reinhardt and Wall (1975) reported S. conulata in only 3 m of the Tomstown Dolomite in central Maryland, where the section is about 150 m thick. The genus is found in several beds through less than 50 m of the Oslobreen Dolomite on northern Spitsbergen, where the unit is about 200 m thick (Gobbert and Wilson, 1960). The longest local stratigraphic section is in the Mackenzie Mountains, Northwest Territories, Canada, where the genus is found in several beds through less than 500 m of the Sekwi Formation (Yochelson and W. H. Fritz, unpublished data). In this area, the Bonnia-Olenellus zone includes more than 1000 m of strata (Fritz, 1976). My impression is that in the areas studied, the oldest Salterella occurs a short distance above the base of this zone, but the genus probably does not extend more than halfway through the rock thickness representing this time interval.

### GEOGRAPHIC DISTRIBUTION

Salterella is known from Europe and North America; outcrop occurrences are plotted on figure 1. I have been able to authenticate these occurrences in part by field studies and in part by laboratory examination. Numbers on figure 1 refer to the following locations: 1) Northwest part of Scottish Highlands (Murchison, 1859) (additional material under investigation); 2) Ny Friesland, Spitsbergen (Hallam, 1958, described, collections at Sedgwick Museum; Ø. Lauritzen and E. L. Yochelson, unpublished data); 3) Ella Ø region, East Greenland (Griffin and Yochelson, 1975 and earlier work listed); 4) Inglefield Land, North-West Greenland (Yochelson and Peel, 1981, and earlier work

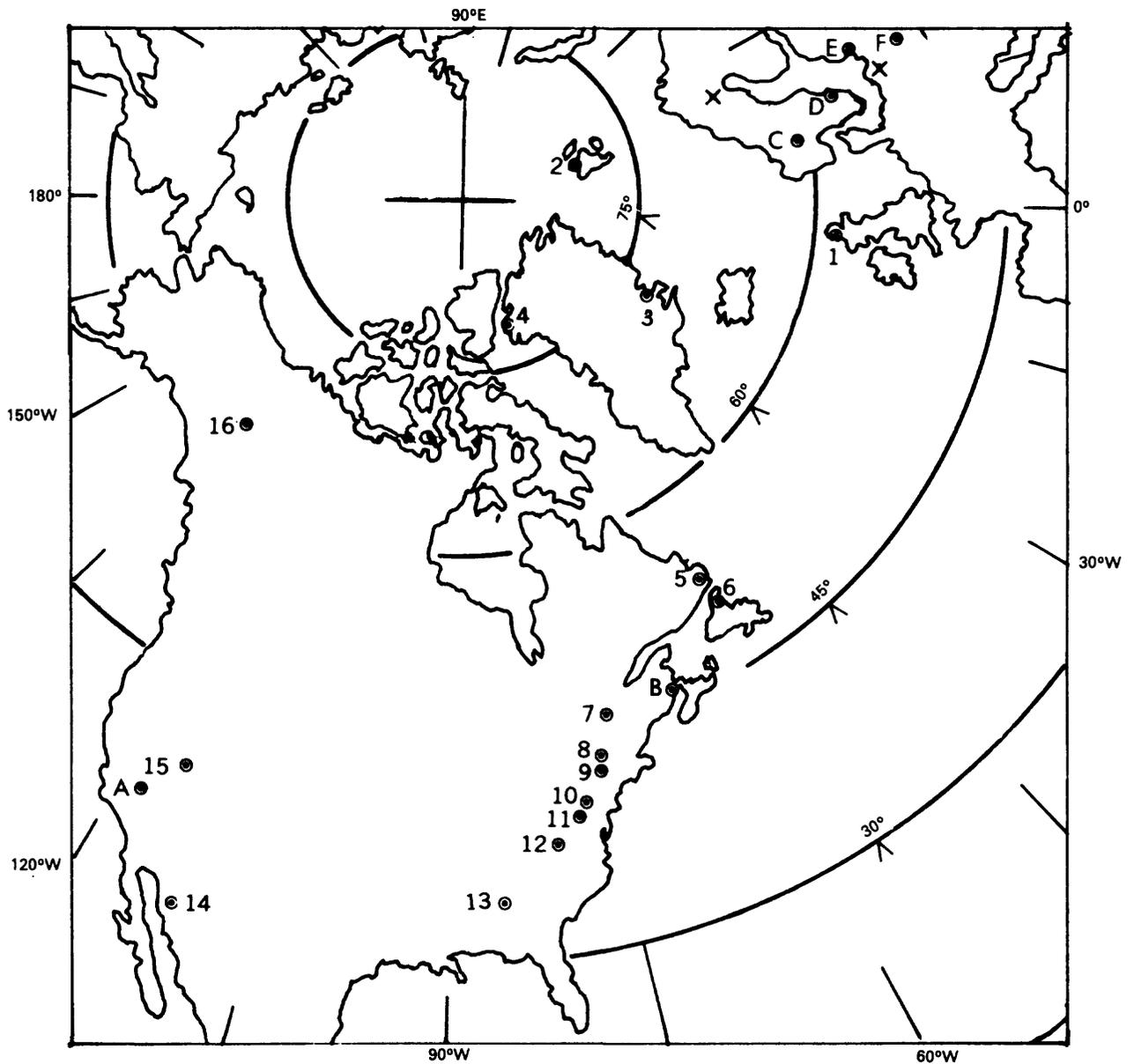


Figure 1.--Outcrop occurrences of *Salterella* (numbers) and *Volborthella* (letters) authenticated by Yochelson; x, *Volborthella* localities not authenticated. Base map modified from National Geographic Society, (1966, p. 11).

listed); 5) Straits of Belle Isle, Labrador (Yochelson, 1977, and earlier work listed); 6) Western Newfoundland (Schuchert and Dunbar, 1934, mentioned; collections at Yale Peabody Museum and N. P. James, Memorial University, Newfoundland, unpublished data); 7) Levis, Quebec (Clark, 1925; collections at Harvard University, Museum of Comparative Zoology); 8) Montpelier, Vermont (G. Theokritoff, Rutgers University, unpublished data); 9) Hoosick quadrangle, New York (Lochman, 1956; figured specimens at U.S. National Museum of Natural History); 10) York, Pennsylvania, and vicinity (Yochelson, 1970, and earlier work listed); 11) Keedysville, Maryland (Reinhardt and Wall, 1975; figured specimens at U.S. National Museum); 12) Austinville, Virginia (Byrd, Weinberg, and Yochelson, 1973); 13) Columbia, Alabama (Butts, 1926, mentioned, collections in U.S. National Museum); 14) Caborca, Mexico, Lochman, 1952; figured specimens at U.S. National Museum); 15) Toquima Range, Nevada (Yochelson, Pierce, and Taylor, 1970); 16) Mackenzie Mountains, Northwest Territories (W. H. Fritz, Geological Survey of Canada, unpublished data).

Several Salterella species were described from Australia, but the species were judged to have been incorrectly assigned (Clark, 1925). Spath (1936) convincingly demonstrated that the Salterella Limestone of Australia is a deposit containing Biconulites, an artificial entity based on current-nested hyoliths. Kobayashi (1937) independently rejected the Australian specimens from the genus. There are no reports of the genus from northern Asia, in spite of intensive investigations of the Early Cambrian in Siberia and China.

#### SPECIES OF SALTERELLA

The species of this genus were last summarized by Clark (1925). Only three general forms of Salterella seem to be known. S. conulata Clark is widespread in the thick carbonate sequence of the Appalachian Mountains (Yochelson, 1970). It may be the oldest form stratigraphically, or it may be facies controlled, confined to areas of magnesian carbonate deposition. Externally, this species is approximately bullet shaped; it has a slow rate of expansion relative to other taxa, and a rounded apex.

S. maccullochi (Murchison), first described from the Scottish Highlands, has been poorly known but is a senior subjective synonym of S. rugosa Billings, from Labrador (Yochelson, unpublished data). S. rugosa in turn is a senior synonym of S. expansa Poulsen from northern Greenland (Yochelson and Peel, 1980). Probably S. mexicana Lochman (1952) is also synonymous with S. maccullochi. Externally, S. maccullochi is slim and expands uniformly at all growth stages; the contents of the inner laminae vary widely among specimens from various localities but are fairly constant among specimens from any one bed.

Finally, there remains the group of S. pulchella Billings, S. curvata Shaler and Foerste, and S. acervulosa Resser and Howell. All have in common a curved shell rather than one radially symmetrical. The individual illustrated by Yochelson (1977, pl. 2, fig. 2) as S. pulchella is not correctly assigned; the species was never illustrated, and the material that Yochelson assumed to be type material does not contain any curved specimens. Sparse curved individuals have been observed in thin sections from some localities, but so far, no topotypes have been found. S. curvata was described from a single specimen, which subsequently has been lost. The species is known only from Hoppin Hill near North Attleboro, Massachusetts, and no additional specimens have been found since the original description. This species might be based on a trilobite spine or hyolith fragment, both of which are abundant at the locality. S. acervulosa is abundant in the Kinzers Formation, near Lancaster, Pennsylvania, but specimens are not well preserved and this species remains poorly known.

#### VOLBORTHELLA

Upon being described, Volborthella Schmidt (1888) almost immediately attracted widespread interest. It was interpreted as the ancestral cephalopod, probably because of its small size and because it has a central tube that simulates a siphuncle and laminae that simulate septae, like a small orthocone. The absence of any calcareous shell in the type or in any of the specimens subsequently described from the Baltic region seems not to have troubled the interpretation. As Clark (1925) showed, weathered silicified specimens of Salterella are far more cephalopod-like than is Volborthella. The general acceptance of the cephalopod interpretations of Volborthella and the general disregard of Salterella until more than half a century after its naming may be a reflection on the importance of the large and active German-speaking community of paleontologists that flourished in Europe around the turn of the century.

Volborthella has been discredited as a cephalopod by most authorities. Glaessner (1976) suggested that it might be assigned to the polychaete annelids. The apparent lack of calcareous shell has been interpreted as a consequence of post mortem solution (Yochelson, Pierce and Taylor, 1970; Yochelson, 1977). Although Volborthella and Salterella have been considered distinct, recent studies (Yochelson, Henningsmoen and Griffin, 1977; Yochelson, 1977) suggest that they may be congeneric.

Further evidence of the identity of Salterella and Volborthella comes from two geographic areas. An extremely well-preserved Volborthella tenuis from Bornholm, Sweden (Yochelson, unpublished data), has the proportions of S. rugosa. More importantly specimens from the Salterella Grit of the Scottish Highlands (Yochelson, unpublished data) are identical with V. tenuis. Associated with these are small wedges of calcium carbonate, which may be the apex of the calcareous outer shell. In the overlying Ghrudaidh Formation, both Volborthella and Salterella occur in the same thin-sections.

Most outcrop occurrences of Volborthella are in Europe (fig. 1), but two North American occurrences demonstrate that Salterella and Volborthella are not confined to different biogeographic provinces. Letters on figure 1 refer to the following locations: A) Inyo Mountains, California (Lipps and Sylvester, 1968; collections at University of California, Davis); B) St. John, New Brunswick (Matthew, 1889, listed; collections at Princeton University); C) Lake Mjøsa area, Norway (Yochelson, Henningsmoen, and Griffin, 1977); D) Island of Öland in glacial drift (Moberg, 1892; collections at Lunds Universitet); E) Tallinn, Estonia (Rožanov, 1979, and earlier works listed; topotypes in U.S. National Museum and at least half a dozen additional institutions); F) Holy Cross Mountains area, Poland (material examined in core in Warsaw).

In addition to these occurrences which I can authenticate, Martinsson (1974) referred to various authors who reported the genus from southern Lapland and in the subsurface of Latvia. I do not doubt these occurrences but use an "X" on figure 1 to indicate that I have not examined specimens. Rozanov (1979) illustrated Latvian specimens and reported the genus in the "Stentokoshisk Mountains", presumably the Holy Cross Mountains. Rozanov accepted a report of Volborthella in the Middle Cambrian of Czechoslovakia that cannot be authenticated (Yochelson, 1977). He did add further evidence confirming the identity of the Early Cambrian Campitius Firby and Durham from Campito Formation in the Inyo Mountains of California with Volborthella (see also Yochelson, 1977).

In the Baltic region, Volborthella is supposed to occur below the Holmia Zone, at least in Scandinavia (Martinsson, 1974). If we accept Volborthella and Salterella as congeneric and if Salterella is as good an index fossil to part of the Bonnia-Olenellus Zone as it appears to be, local correlations of the Early Cambrian in the Baltic platform and Scandinavia may be one or two stages too low. In view of the sparse Early Cambrian fossil record of that region, this suggested revised correlation should be seriously evaluated. According to Lipps and Sylvester (1968), their Volborthella specimens from California occur above Holmia, another indication that some Early Cambrian correlations may be awry. One Norwegian zonation scheme does list Callavia with Volborthella (Skjeseth, 1963).

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## 70. DISCOVERY OF THE TOMMOTIAN FAUNA IN SOUTHWEST CHINA AND ITS BEARING ON THE PROBLEM OF THE PRECAMBRIAN-CAMBRIAN BOUNDARY

By

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Opinions concerning the position of the Precambrian-Cambrian boundary in China are varied. Zhong Hua (1977), Qian Yi (1977, 1978), Yu Wen (1979), and Tsao Renguan (1980) considered that the base of the Meishucun Stage, with its abundant shelly faunas, is the base of the Cambrian System in China. Members of the Research Group of the Yangtze Gorge District organized by the Hubei Geological Bureau (1978) are of the opinion that the boundary may be drawn below the lowest trilobite zone at the base of the Chiungchussu Formation. The Meishucun Stage, which is underneath the Chiungchussu Formation, is not included by them in the Cambrian, but is placed instead in the Precambrian Sinian System.

In a paper entitled "Lower Cambrian Archaeocyathid Assemblages of Central and SW China" (in press), which follows a comprehensive study of the archaeocyathid faunas, we stated the following conclusions: (1) The Lower Cambrian archaeocyathid faunas in central and southwest China may be divided into four assemblages in descending order: (a) the Tienheban, (b) the Yingzuiyan (or the Chingtingshan), (c) the Liangshuijing (or the Xiannandong or the Jinsha), and (d) the Chiungchussu Assemblages. (2) A tentative correlation of Lower Cambrian strata between central China, southwest China, and Siberia may be found in the fact that the Tienheban Assemblage corresponds to the early Lenian Stage, the Yingzuiyan and the Liangshuijing ones coincide with the Atdabanian Stage, and the Chiungchussu Assemblage is considered to be the Tommotian Stage. Moreover, the oldest archaeocyathid fauna of Morocco may be assigned a position between the Yingzuiyan and the Liangshuijing Assemblages. (3) It is possible that the trilobite-

bearing Chiungchussu Stage corresponds to part of the Tommotian, and that at least a part of the Meishucun Stage is older than the Tommotian.

Recently we have studied small shells, fossils from limestones that bear the Liangshuijing archaeocyathid assemblage. The rich fauna contains Tommotia, Fomitchella, Cirotheca, Trapezotheca, Anabarella, Bemalla, Igorella, Latouchella, and others. This assemblage shows strong affinities to faunas of the Tommotian Stage of Siberia, but it does not occur in the Meishucun Stage of Yunnan, nor in the corresponding Meideiping Stage of Western Szechuan, nor in the younger Huangshandong Member of the Yangtze Gorge. The genera Tommotia, and Fomitchella and so on are regarded as the important fossils of the Tommotian Stage. Therefore, the Tommotian of Siberia may be correlated with the Liangshuijing Assemblage of central and southwest China. Thus, the Tommotian is not considered the equivalent of the Meishucun Stage. The Meishucun Stage must be regarded as the oldest Cambrian sequence in the world. In Siberia, the existence of a lithologic and stratigraphic break or unconformity between the Tommotian and the Precambrian Yudomian is remarkable (Savitsky, 1978). The hiatus probably represents the time of deposition of the Meishucun Stage and at least part of the Chiungchussu Assemblage as well. Although the Tommotian has been regarded by some as the stratotype of the lowest Cambrian, it is much younger than the Meishucun Stage. Therefore the Meishucun Stage should be regarded as the stratotype of the lowest Cambrian.

## 71. THE BIOSTRATIGRAPHIC DISTRIBUTION OF LOWER CAMBRIAN TRILOBITES IN SOUTHWEST CHINA

By

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Three stages and eleven biochronozones are recognized in the Lower Cambrian trilobite-bearing strata of southwest China. In descending order, they are:

### LUNGWANGMIAO STAGE

11. Redlichia quizhouensis Zone
10. Redlichia murakamii-Hoffetella Zone

### TSANGLANGPU STAGE

9. Megapalaeolenus Zone
8. Palaeolenus Zone
7. Paokannia-Sichuanolenus Zone
6. Metaredlichioides-Chengkouia Zone
5. Drepanuroides Zone
4. Yunnanaspis-Yiliangella Zone

### CHIUNGCHUSSU STAGE

3. Yunnanocephalus-Malungia Zone
2. Eoredlichia-Wulingaspis Zone
1. Parabadiella-Mianxiandiscus Zone

The distribution of the key trilobite genera and subgenera in each biochronozone are given in figure 1.



## 72. CAMBRIAN WORLD PALEOGEOGRAPHY, BIOGEOGRAPHY AND CLIMATOLOGY

By

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Paleomagnetic studies suggest that a supercontinent existed in the late Precambrian, that there was a breakup about the beginning of the Cambrian, and that the individual paleocontinents moved at considerable rates during the Cambrian (Ziegler and others, 1979). By the Late Cambrian, at least five continents can be identified: Gondwana, Baltica, Laurentia, Siberia, and Kazakhstania-China. These all occupied relatively low latitudes, leaving open polar oceans above lat 60° N. and S.

Cambrian workers have defined at least six biogeographic provinces, the American, Siberian, European, and Hwangho, which represent shallow conditions, and the Acado-Baltic and Chiangnan, which are open ocean faunas (Ziegler and others, 1981). On maps (Ziegler and others, 1979), the American and Siberian provinces occupy the tropical zone, the European and Hwangho provinces the south and north temperature zones, respectively, and the Acado-Baltic and Chiangnan provinces the south and north subtropical gyres, respectively.

The remarkable paleogeographic features of the Late Cambrian, for example land areas limited to low latitudes and open high-latitude and polar oceans, made the Late Cambrian climatologically unique. Prevailing winds and ocean currents would have been almost wholly zonal, that is, parallel to latitude, especially above 50°-60° N. and S. (Ziegler and others, 1981). This prediction is based on the assumption that

the general structure of the atmospheric circulation has not changed radically, even with the higher speed of rotation of the Earth in the Cambrian, an assumption that is borne out by the distribution of phosphorites (which are ultimately climatically controlled) and the biogeographic provinces. Recent heat budget calculations indicate that the peculiar distribution of land and sea in the Late Cambrian meant that absorbed solar radiation was lower than for any other time in the Phanerozoic, save for the latest Ordovician glacial episode. Furthermore, if solar luminosity was significantly (2-3 percent) lower in the Cambrian, as several workers believe, the Cambrian was a very cool period indeed.

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