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PALEOBIOGEOGRAPHY OF LATE PERMIAN BRYOZOA

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Abstract: Bryozoa flourished during the Wordian and Early Capitanian Stages of the Late Permian throughout the world. Many of these bryozoans gradually became extinct during the Capitanian, Wuchiapingian and Changhsingian Stages with only four genera surviving into the Triassic. This gradual reduction of bryozoan genera during the Late Permian and the survival of at least four genera into the Triassic does not support a sudden extinction event at the end of the Changhsingian for this group of organisms.

Keywords: Permian, bryozoan, paleobiogeography

INTRODUCTION

Although there have been a number of papers published on the stratigraphic and paleobiogeographic distributions of Permian bryozoans in the past twenty years (Sakagami, 1976, 1985; Ross, 1978; Ross and Ross, 1990; Bambach, 1990), the most comprehensive account of Late Permian bryozoans was published by Morozova (1970). The present paper is an update of Morozova's work along with the addition of paleogeographic maps using the paleobiogeographic designations proposed by Ross and Ross (1990) and the most recent correlations for the late Permian proposed during the Permian Symposium held in Guiyang, China (Jin Yugan and others, 1994a; Jin Yugan and others, 1994b).

A number of problems became evident when attempting this type of comprehensive compilation of widespread and diverse faunal data. The most significant problems are the lack of taxonomic uniformity throughout the study of bryozoans; difficulties in making stratigraphic correlations to a standardized scale, especially with the older literature; and geographically locating the described faunas on present day maps, let alone Permian paleobiogeographic maps.

As far as the taxonomic resolutions are concerned, the two senior authors have attempted to resolve synonymies and present generic distributions based on the most up-to-date understanding of the taxonomy of Late Permian bryozoans. This includes recent revisions of the genus *Fenestella* by Morozova (1974), and incorporates some of the revisions necessitated by the classification of Snyder (Snyder, 1991; McColloch and others, 1994). Similar revisions in the polyporids are also needed to make the polyporid data more meaningful for paleobiogeographic interpretation.

Correlation of various published faunas to a standardized Late Permian time scale is very difficult. The present adopted standardized scale for this study is based on a scale determined by conodont zonation (Fig. 1). The ages of many of the original bryozoan studies were determined by using zonations based on various groups such as fusulinids, cephalopods, corals, or brachiopods. With a lack of conodont information for many of these studies, some of the correlations to a standardized scale are only best approximations.

Another difficulty is the designation "Late Permian" bryozoans. We use a "two-fold" designation for the Permian instead of a "three-fold" division and select the boundary between the Cathedralian and the Wordian as the Lower Permian-Upper Permian boundary. In the papers by Sakagami (1976; 1985), he designated Late Permian bryozoans as those bryozoans occurring in Ochoan, Tartarian, Lopingian, and Dzhulfian rocks. His papers do not include those bryozoans from the older Guadalupian, Kazanian, Maokouan, and Murgabian rocks of the present report. This major difference in definition makes it difficult to compare general conclusions on Late Permian bryozoans between Sakagami's studies and our present study. Also, in Ross and Ross (1990), they list Ufimian-Roadian bryozoans between Early and Late Permian with dashed lines in their figures and it is not possible to tell from the diagram or the text whether these bryozoans are considered Early or Late Permian in age.

SYSTEM	SERIES		STAGE	CONODONTA
TRIASSIC			Griesbachian	*Hindeodus parvus*
PERMIAN	UPPER PERMIAN	Lopingian	Changhsingian	*Clarkina subcarinata*
			Wuchiapingian	*Clarkina postbitteri*
		Guadalupian	Capitanian	*Jinogondolella postserrata*
			Wordian	*Jinogondolella aserrata*
			Roadian	*Jinogondolella nankingensis*
	LOWER PERMIAN		Cathedralian	

Fig. 1 Chronostratigraphic scheme of the Late Permian with conodont index species.

We have chosen to use a modified version of the paleogeographic maps of Scotese and McKerrow (1990) and Nie and others (1990) for our Late Permian reconstruction (Fig. 2). We have attempted to locate all of the published bryozoan faunas on this map using the paleobiogeographic regions and subdivisions used by Ross and Ross (1990).

THE DEMISE OF THE BRYOZOANS IN THE LATE PERMIAN

Based on our generic compilation (Fig. 3), there are 101 genera of Late Permian bryozoans: 41 genera in the Roadian; 82 genera in the Wordian; 84 genera in the Capitanian; 35 genera in the Wuchiapingian; and 12 genera in the Changhsingian. Although *Dyscritella*, *Paralioclema*, and *Pseudobatostomella* have not been reported from Changhsingian rocks, they are reported from

Wuchiapingian and Triassic rocks and must have lived during the Changhsingian. Therefore, these three genera have been included in the total reported from the Changhsingian. Of the 101 genera of bryozoans in the Late Permian, only 17 genera are found to be restricted to a single stage.

Several conclusions result from examining the generic distributions in Fig. 3. The maximum generic diversity of bryozoans in the Late Permian occurred during the Wordian and Capitanian Stages. The number of genera present in the Roadian and the Wuchiapingian is about the same and approximately half of that present in the Wordian and Capitanian. And finally, the number of genera present in the Changhsingian is greatly reduced compared to the other stages. This supports the conclusions of Ross and Ross (1990) that "...the remaining survivors of the Guadalupian suffered extensive extinctions before the end of the Permian."

Beginning with th e Capitanian, more than half the genera have become extinct by Wuchiapingian time, and from Wuchiapingian to Changhsingian, we see an additional two-thirds becoming extinct until only four genera are still present in the Triassic (Fig. 3). Three of the four genera (*Dyscritella*, *Paralioclema*, and *Pseudobatostomella*) were reported from Early Permian rocks and the fourth genus (*Articopora*) was reported from as early as Wordian time. In other words, the four genera that survived into the Triassic lived throughout the Late Permian. This extinction occurs over a period of approximately 15-16 million years using the approximate time values given to the upper half of the Late Permian by Menning (1992). Although this is a relatively short period of time geologically, it is a significantly longer amount of time than some workers propose for the "extinction event" at the end of the Permian. What the distribution of bryozoans in the Late Permian appears to indicate is a decrease in number of genera beginning with the Capitanian and continuing on through the Wuchiapingian and Changhsingian into the Triassic, and not a sudden extinction event at the end of the Changhsingian.

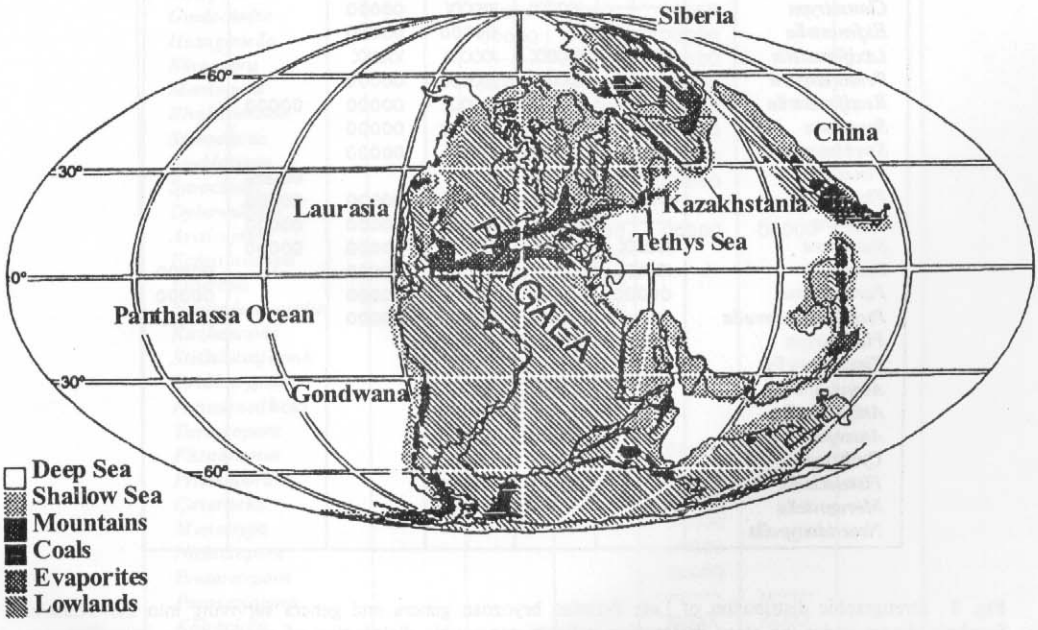

Fig. 2 Paleogeographic reconstruction for the Late Permian (modified from Scotese and McKerrow, 1990; and Nie Shang-you and others, 1990).

Genera	Upper Permian					Triassic
	Roadian	Wordian	Capitanian	Wuchiapingian	Changhsingian	
Iraidina	00000					
Parametelipora	-------					
Paucipora	00000					
Alternifenestella	-------	00000				
Filites	00000	00000				
Gilmoropora	-------	-------				
Hyphasmopora	XXXXX	XXXXX				
Lyrocladia	-------	-------				
Permoheloclema	-------	-------				
Maychellina	XXXXX	00000	00000			
Pamirella	-------	XXXXX	XXXXX			
Permofenestella	-------	-------	00000			
Ptylopora	-------	-------	-------			
Ramipora	XXXXX	-------	-------			
Rhombopora	00000	XXXXX	XXXXX			
Rhombotrypella	-------	-------	-------			
Timanodictya	-------	XXXXX	XXXXX			
Wjatkella	-------	-------	-------			
Dyscritellina	-------	XXXXX	00000			
Fabifenestella	-------	-------	00000			
Girtypora	00000	XXXXX	XXXXX			
Hinganotrypa	00000	00000	00000			
Maychella	-------	00000	00000			
Polyporella	-------	XXXXX	XXXXX			
Primorella	-------	XXXXX	XXXXX			
Spinofenestella	-------	00000	00000			
Tabulipora	XXXXX	XXXXX	XXXXX			
Clausotrypa	-------	XXXXX	XXXXX	00000		
Exfenestella	-------		00000	00000		
Laxifenestella	XXXXX	XXXXX	XXXXX	XXXXX		
Penniretepora	-------	XXXXX	XXXXX	00000		
Rectifenestella	-------	-------	XXXXX	00000	00000	
Septopora	-------	XXXXX	00000	00000		
Streblascopora	XXXXX	XXXXX	XXXXX	00000		
Fenestella	-------	XXXXX	XXXXX		00000	
Fistulipora	00000	XXXXX	XXXXX	00000	00000	
Polypora	-------	XXXXX	XXXXX	00000	00000	
Stenopora	XXXXX	XXXXX	XXXXX	00000	00000	
Dyscritella	XXXXX	XXXXX	XXXXX	00000		00000
Paralioclema	00000	XXXXX	XXXXX	00000		00000
Pseudobatostomella	-------	XXXXX	XXXXX	00000		XXXXX
Fistulotrypa		00000				
Flexifenestella		-------				
Acanthocladia		XXXXX	XXXXX			
Anisotrypella		-------	-------			
Araxopora		00000	00000			
Cyclotrypa		XXXXX	XXXXX			
Fistulocladia		00000	00000			
Morozoviella		-------	-------			
Neoeridotrypella		-------	-------			

Fig. 3 Stratigraphic distribution of Late Permian bryozoan genera and genera surviving into the Triassic. Symbols shown under the stage designation indicate geographic distribution of genera: ------- non-Tethyan; xxxxx non-Tethyan and Tethyan; ooooo Tethyan.

Fig. 3 (Continued)

Genera	Upper Permian					Triassic
	Roadian	Wordian	Capitanian	Wuchiapingian	Changhsingian	
Neorhombopora		-------	-------			
Parafenestralia		-------	-------			
Permolioclema		00000	00000			
Permopora		00000	00000			
Pictatella		-------	-------			
Pinegopora		-------	-------			
Pustulopora		00000	00000			
Reteporidra		XXXXX	XXXXX			
Rhombofenestella		00000	00000			
Ropalonaria		00000	00000			
Rugofenestella		00000	00000			
Shulgapora		00000	00000			
Sulcoretepora		00000	00000			
Thamniscus		XXXXX	XXXXX			
Timanotrypa		-------	-------			
Triznella		-------	-------			
Ulrichotrypa		00000	-------			
Fistulamina		00000	00000			
Hayasakapora		00000	00000			
Hinganella		XXXXX	-------			
Ogbinopora		00000	00000			
Ulrichotrypella		XXXXX	XXXXX			
Coscinotrypa		XXXXX	00000	00000		
Eridopora		00000	00000	00000		
Girtyporina		XXXXX	XXXXX	00000		
Goniocladia		XXXXX	XXXXX	00000		
Hexagonella		00000	00000	00000		
Kingopora		-------	-------	00000		
Meekopora		XXXXX	XXXXX	00000		
Rhabdomeson		XXXXX	XXXXX	00000		
Stenodiscus		00000	00000	00000		
Streblotrypa		XXXXX	XXXXX	00000		
Synocladia		XXXXX	00000	00000		
Dybowskiella		00000		00000	00000	
Arcticopora		00000	00000	00000	00000	-------
Epiactinotrypa			00000			
Etherella			00000			
Neoeridocampylus			00000			
Ruzhencevia			00000			
Stellahexaformis			-------			
Streblotrypella			00000			
Parastenodiscus			00000			
Tavayzopora			00000			
Fistuliramus			00000	00000		
Prismopora			00000	00000		
Cavernella				00000		
Monotrypa				00000		
Nicklesopora				00000		
Protoretepora				00000		
Paraseptopora				-------	-------	
Kalvariella				XXXXX	XXXXX	

PALEOGEOGRAPHIC DISTRIBUTION OF LATE PERMIAN BRYOZOA

The Late Permian reconstruction (Fig. 4) shows the number of genera reported from each major faunal locality. These faunal localities correspond in general to the paleobiogeographic regions and subdivisions used by Ross and Ross (1990). By dividing the three Tethyan regions (northern, central, and southern) into their geographic subdivisions and showing the number of genera in each subdivision, the diversity of genera present in each locality is similar to areas outside the Tethyan regions. The only exception is in the northern Tethys where 51 genera are present in the Primoria area. If this is not simply a monographic anomaly, it may have been a major center for bryozoan diversification during the Late Permian.

Using a similar approach to Sakagami (1976), we have plotted the paleobiogeographic distributions of several genera during the Late Permian. Unlike Sakagami who plotted his distributions on a present day map, we have used a Late Permian reconstruction (Figs. 5-8). These maps depict our present knowledge about generic distributions and will probably change as various workers study faunas from Australia, New Zealand, Canada, China, and the United States, just to name a few of the many geographic areas where Late Permian bryozoans are poorly known.

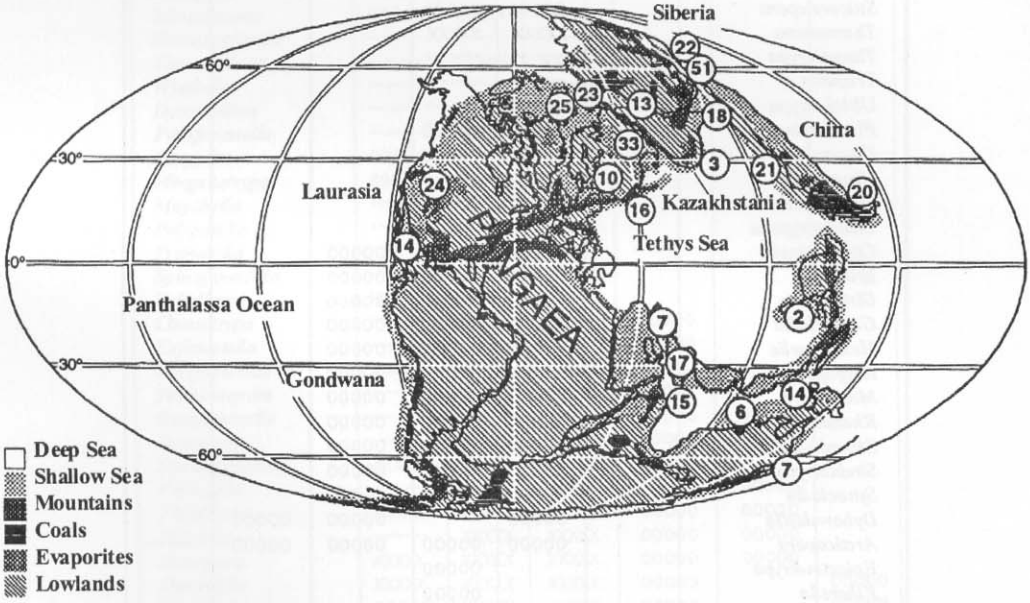

Fig. 4 Paleogeographic map showing total number of genera reported in each faunal locality for the Late Permian.

ORIGIN AND DISPERSAL OF LATE PERMIAN BRYOZOAN GENERA

Both the geographic and stratigraphic distributions of *Stenopora*, *Dyscritella*, and *Pseudobatostomella* were extensive during the Late Permian (Figs. 3;5). All three genera are found in non-Tethyan and Tethyan regions and range from Roadian to Wuchiapingian in age. *Stenopora* has been reported from Changhsingian rocks and *Dyscritella* and *Pseudobatostomella* must have been present in the Changhsingian as noted previously. *Stenodiscus* is restricted to the Tethyan regions (Fig. 8) and has been reported from Wordian through Wuchiapingian rocks. However, because this genus is common in Early Permian and Carboniferous rocks, it must have lived during the Roadian Stage, too.

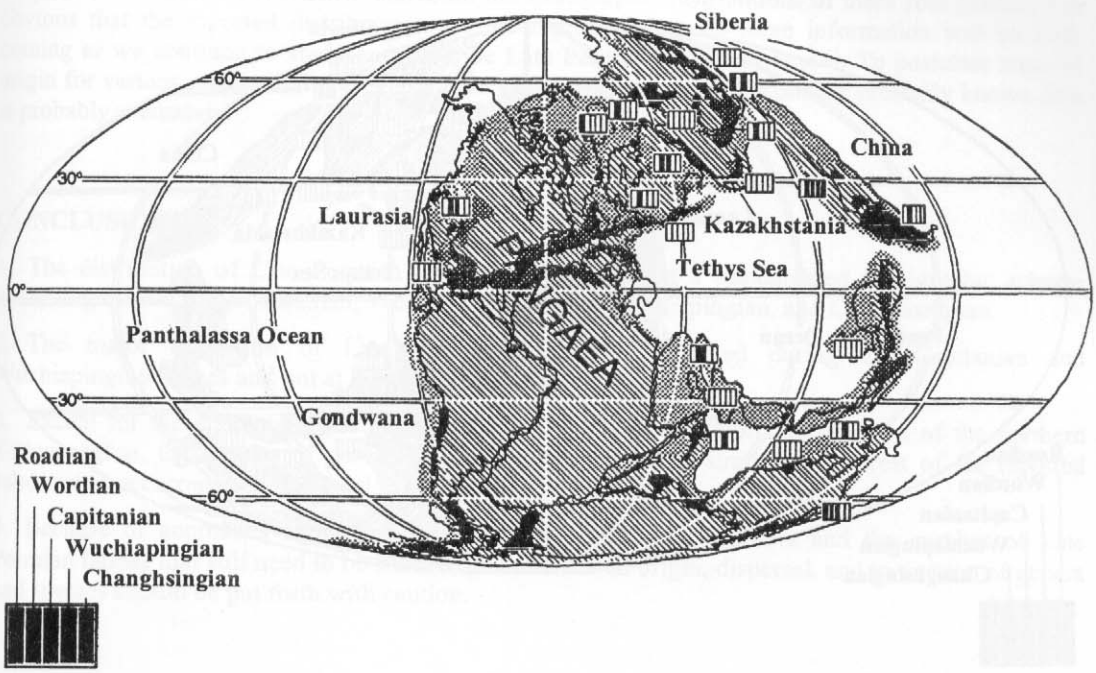

Fig. 5 Distribution of the bryozoan genus *Stenopora* in the Late Permian. Black vertical bars indicate presence of genus during each Late Permian stage at that location.

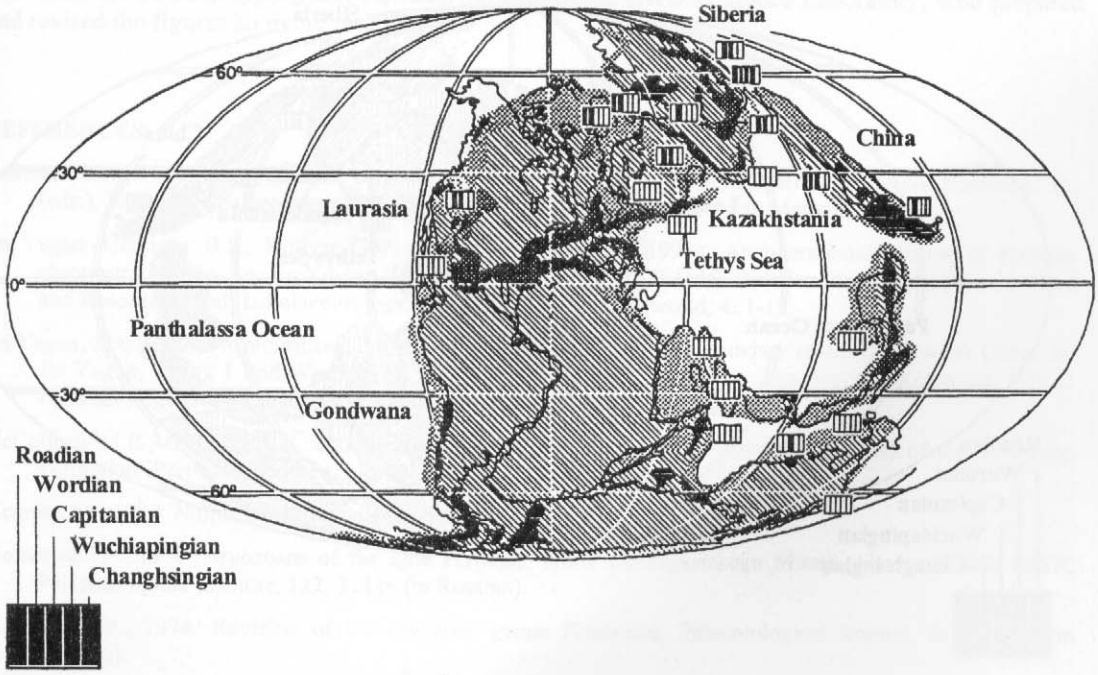

Fig. 6 Distribution of the bryozoan genus *Dyscritella* in the Late Permian. (For legend explanation, see Fig. 5)

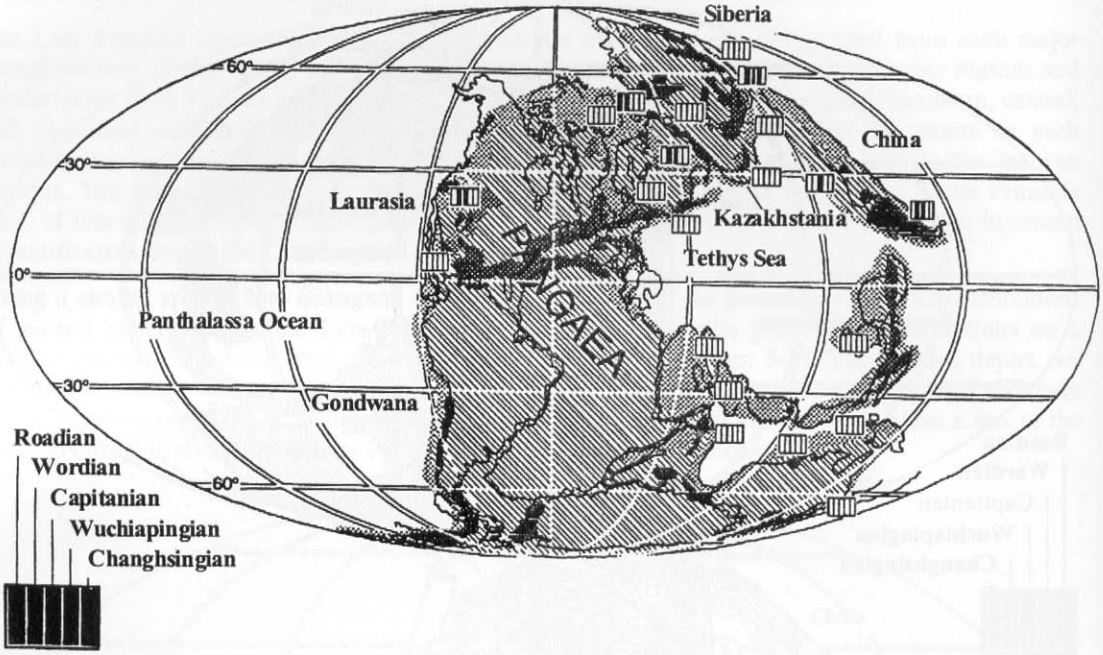

Fig. 7 Distribution of the bryozoan genus *Pseudobatostomella* in the Late Permian. (For legend explanation, see Fig. 5)

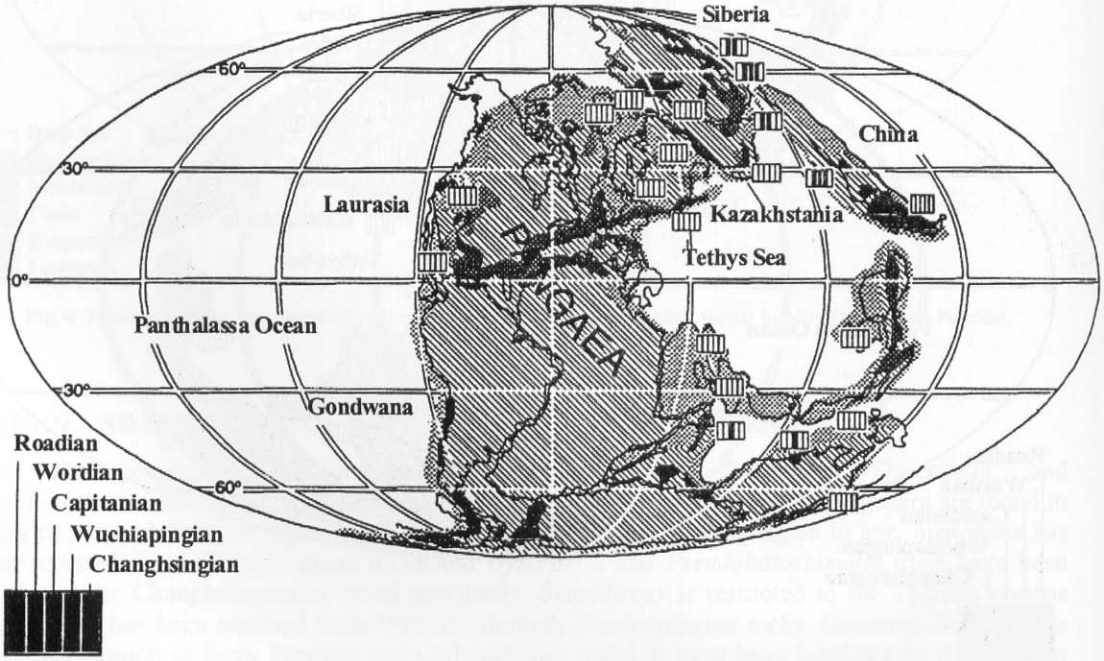

Fig. 8 Distribution of the bryozoan genus *Stenodiscus* in the Late Permian. (For legend explanation, see Fig. 5)

Based on the conclusions reached above on the stratigraphic distributions of these four genera, it is obvious that the reported distributions are incomplete and much more information will be forth coming as we continue to study and describe Late Permian bryozoan faunas. To postulate areas of origin for various genera and their geographic dispersal through time from the presently known data is probably premature.

CONCLUSIONS

1. The distribution of Late Permian bryozoans is shown on a standardized stratigraphic scheme consisting of five stages: Roadian, Wordian, Capitanian, Wuchiapingian, and Changhsingian.

2. The major extinction of Late Permian bryozoans occurred during the Capitanian and Wuchiapingian Stages and not at the end of the Changhsingian Stage.

3. Except for the anomalous occurrence of 51 genera in the Primoria subdivision of the northern Tethys region, the density of genera in the Tethyan regions is similar to the rest of the reported subdivision occurrences in the world.

4. Because of anomalies in the reported occurrences of certain genera and the number of Late Permian faunas that still need to be studied, postulations on origin, dispersal, and extinction of genera and species should be put forth with caution.

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