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Stages in Evolution and Biogeography of Permian Ammonoids

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Abstract—The generic diversity of Permian ammonoids is analyzed, and four evolutionary stages of the fossils are distinguished. The diversity dynamics is elucidated for five principal distribution areas: the Paleotethyan, Uralian, American, Arctic, and Australian provinces. Certain trends of ammonoid biogeographic distribution are characterized for principal stages of their evolution.

Key words: *biogeography, ammonoids, evolutionary stages, Permian*

INTRODUCTION

Ammonoids represent the relatively well-studied group of fossils of high stratigraphic potential for subdivision and correlation of Upper Paleozoic deposits, Permian in particular, but despite this, the biogeographic distribution of these pelagic (or benthonic–pelagic) organisms has so far been inadequately studied. The problem has been analyzed only for certain time intervals of the Permian System in separate areas (Zhou, 1986; Spinosa *et al.*, 1991; Bledinger *et al.*, 1992; and others). The circumstantial paper by Nassichuk (1995) is devoted to detailed characteristics of Permian ammonoid fauna from the Arctic regions of the globe. A group of Chinese and American scientists (Zhou *et al.*, 1996) have recently analyzed the evolutionary changes of ammonoids, disregarding their geographic differentiation. Unfortunately, they excluded the Kungurian Age from consideration and thus presented the less precise and unfinished general evolutionary patterns of ammonoids. It is also difficult to agree with the taxonomy and stratigraphic ranges of many Permian ammonoid taxa accepted in their work, as these issues are considered at the knowledge level of the 1960s.

This study is aimed, first of all, to generalize the available data on geographic ranges of Permian ammonoids, although this problem cannot be fully solved at present. Natural zones of the Permian epoch were much more differentiated as compared to those of the Carboniferous. The Permian evolution history of ammonoids was quite variable, full of significant events, some of which were dramatic (the appearance of the new ammonoid order Ceratitida at the Early–Late Permian boundary and the almost complete extinction of the whole subclass near to the Permian–Triassic boundary). Biogeographic connections remained unstable during the Permian and changed from one stage to another in the course of ammonoid evolution.

EVOLUTIONARY STAGES OF PERMIAN AMMONOIDS

At the commencement of the Permian, the most widespread were representatives of ammonoid orders Goniatitida and Prolecanitida, consisting of mostly families and genera inherited from the Carboniferous. The very beginning of the Permian was marked by the appearance of four new families: Paragastrioceratidae (genus *Svetlanoceras*), Metalegoceratidae (genus *Juresanites*), Perrinitidae (genus *Properrinites*), and Popanoceratidae (genus *Protopopanoceras*). In addition, some new genera appeared in two families that had existed before: genus *Kargalites* amid Marathonitidae, and genera *Prostacheoceras* and *Tabantalites* amid Vidrioceratidae.

In analyzing changes in the generic diversity, morphological evolution, and events of mass extinction, I distinguished four principal stages of the Permian ammonoid history (Fig. 1). Four evolutionary stages have been also recognized in the history of other marine invertebrates, such as fusulinids, conodonts, and brachiopods (Leven *et al.*, 1996).

The first "pro-Permian" stage spans the interval of the Asselian and Sakmarian ages, together with a part of the Artinskian Age. In general, the ammonoid genera of this period were rather similar in taxonomic composition and morphology to the Carboniferous ancestors. Their evolution was characterized by a considerable growth of taxa (more than twice) in both aforementioned orders. The total number of genera increased from 17 to 37: from 12 to 25 in the order Goniatitida (13 new genera) and from 5 to 12 in the order Prolecanitida (7 new genera). The greater taxonomic diversity was accompanied by a certain sophistication of morphology as compared to that of the Carboniferous goniatites, who mostly had the eight-lobe septa (in the suture of goniatites from families Marathonitidae, Vidrioceratidae, and Shumarditidae, the amount of lobes becomes greater and these elements show the secondary segmentation like in representatives of newly appeared families). The development of a more sophisticated hydrostatic apparatus allowed ammonoids to better adapt to the diverse habitat environments. The significant extinction at the end of the first stage primarily hit genera originated in the Carboniferous.

The second "eo-Permian" stage spanning the Artinskian (partly) and Kungurian ages is characterized by the evolution of typical Permian goniatites and prolecanites. New genera, which appeared during this stage, represent almost 60% relative to the total number of generic taxa, whereas genera inherited from the Carboniferous exemplify less than 10%. The taxonomic diversity of both ammonoid orders grew further and was at its peak in the Kungurian Age. The total number of genera (Fig. 1) was 55 in the Artinskian Age (36 of goniatites and 19 of prolecanites) and 71 in the Kungurian time (57 of goniatites and 14 of prolecanites). The diversification progressed together with the significant morphological sophistication (among goniatites, there appeared the genus *Perrinites* with the "ammonite" suture, first multilobate *Stacheoceras* forms, and genera *Popanoceras* and *Thalassoceras* displaying the extremely segmented lobes; newcomers of prolecanites were genera *Bamyaniceras* and *Sicanites*, and also complex *Medlicottia* and the first *Eumedlicottia* forms).

The third "meso-Permian" stage corresponds to the interval of the Roadian and Capitanian ages (I consider the latter in a broad sense as including the Amarassian Stage). The main event of this period was the appearance of the first representatives from the genus *Paraceltites* of the new ammonoid order Ceratitida; these forms were initially primitive and scarce. Goniatites and prolecanites of that time showed the most complicated morphology (family Cyclolobidae of goniatites with genera *Waagenoceras, Timorites*, and *Cyclolobus*, and also genera *Eumedlicottia, Neogeoceras*, and some others of prolecanites), although there was a distinct tendency in the diversity decrease in both groups of fossils. In general, 50 Roadian genera (40 of goniatites, 9 of prolecanites, and one of ceratites), 50 Wordian genera (39 of goniatites, 8 of prolecanites, and 3 of ceratites), and only 24 Capitanian genera (16 of goniatites, 5 of prolecanites, and 3 of ceratites) have been identified.

The fourth "meta-Permian" stage spans the two last ages of the Permian: Dzhulfian and Dorashamian (or Wuchapingian and Changsingian, according to the scale suggested by the International Subcommission on Permian Stratigraphy). The wide distribution and abundance of diverse ceratites in the eastern Paleotethys, together with the parallel decline of goniatites and prolecanites, were the most characteristic features of the stage. Ammonoids of two latter groups became extinct almost entirely at the Permian–Triassic boundary. The abundance parameters for the fourth stage are as follows: 47 Dzhulfian genera (11 of goniatites, 4 of prolecanites, and 32 of ceratites) and 29 Dorashamian genera (4 of goniatites, one of prolecanites, and 24 of ceratites).

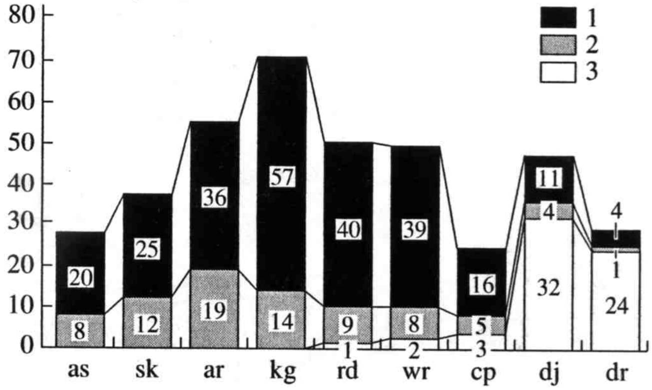

Fig. 1. Changes in generic diversity of Permian ammonoids across stages of the Permian System: (1) goniatites; (2) prolecanites; (3) ceratites. Stages: (as) Asselian; (sk) Sakmarian; (ar) Artinskian; (kg) Kungurian; (rd) Roadian; (wr) Wordian; (cp) Capitanian; (dj) Dzhulfian; (dr) Dorashamian.

Only two ceratitid genera crossed the Permian–Triassic boundary, but their representatives violently evolved and experienced extreme diversification during the Triassic. The last goniatites are known from the Dorashamian (Changsingian) deposits, and only one prolecanitid taxon (genus *Episageceras*) was able to survive this stage, though it disappeared soon thereafter and left no descendants.

BIOGEOGRAPHIC ANALYSIS

Experts in ammonoids used to consider two large distribution areas of their Permian representatives: Boreal (high latitudes with temperate climate) and Tethyan (warm-water basins of low latitudes) provinces. This subdivision seems to be quite conventional, and Nassichuk (1995) is obviously right in stating that the general term "Boreal province" denotes territories adjacent to the Arctic ocean, although there are exceptions (Nevada, North California, northern China). The Tethyan province is not well defined in the paleogeographic sense. Its separate areas recurrently changed their position in the course of geological history, so it is often difficult to understand where sediments bearing this and that fauna have been accumulated. The distribution of Paragastrioceratidae forms in "Boreal" regions and Perrinitidae species in "Tethyan" areas is usually considered as one of basic criteria discriminating different habitat zones of ammonoids. This discrimination is not unambiguous, however, because it is established that representatives of these two families coexisted in several regions. Besides, the Urals are known as a center of diversification and maximum abundance of paragastrioceratids cannot be attributed

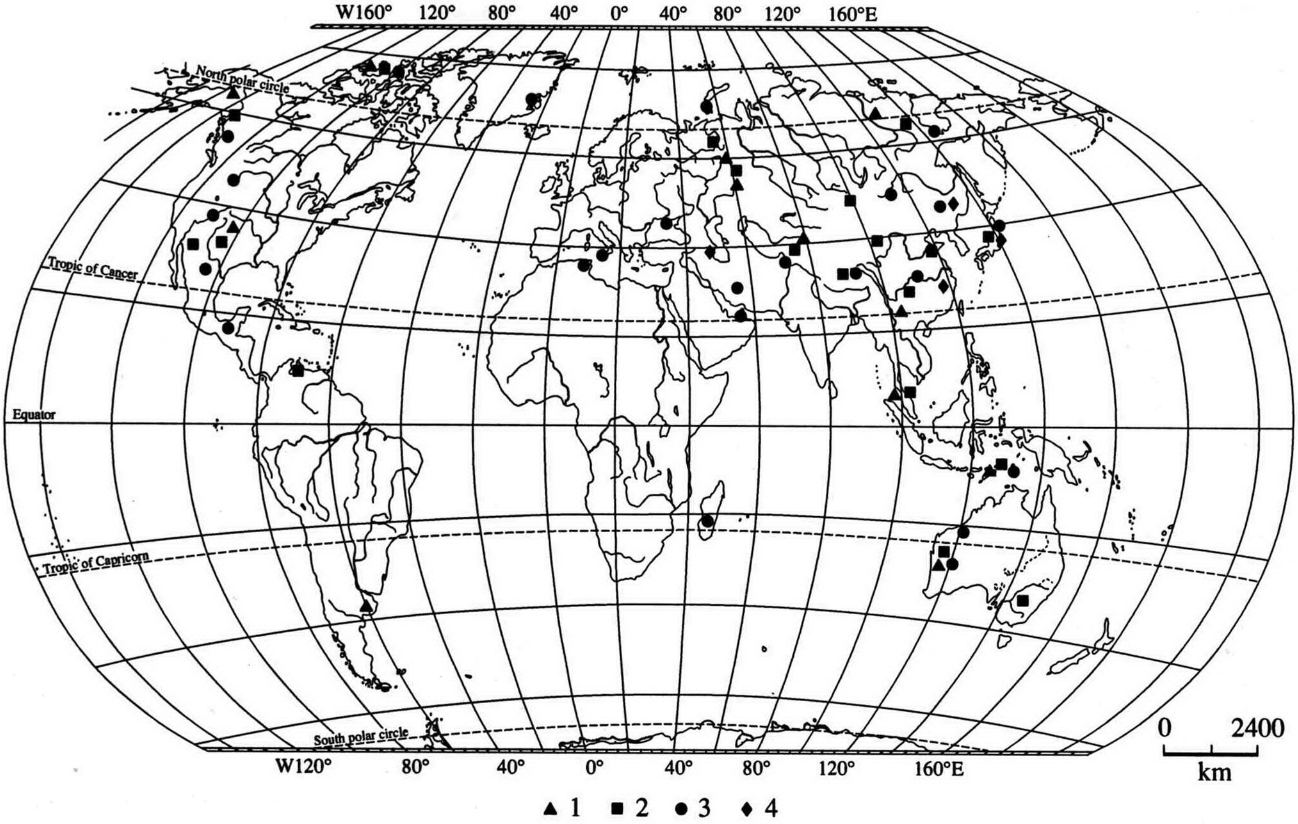

Fig. 2. Main localities of Permian ammonoids: (1) first stage; (2) second stage; (3) third stage; (4) fourth stage.

unconditionally to the regions of the first type, although many researchers consider it as a part of the Boreal (Spinosa *et al.*, 1991; Nassichuk, 1995; and others) or Biarmian province (Ganelin and Kotlyar, 1984). At the very beginning of the Permian, the Uralian basin was freely connected with the Paleotethys, since the ammonoid species from genera *Synartinskia* and *Daixites*, both considered as typical endemics of the Early Permian fauna of the Urals, were also found in the Sakmarian deposits of the Darvaz (Leven *et al.*, 1992). Moreover, the genus *Cardiella*, widespread in basins of the Paleotethys, is known from the Artinskian sediments of the Urals. In the second half of the Early Permian, the connection between the Uralian basin and northern Paleotethys was destroyed. Data pointing to any connection between the Uralian and Boreal basins in the earliest Permian are unknown. Basins with fauna of the Boreal type were formed in the north of the Urals only at the end of the Early Permian. As for the American basins, the general opinion is that they were outside of the Tethyan province and populated by diverse ammonoid communities, the abundant perrinitids inclusive (Leonova, 1996). One may regard the differentiation of "Boreal" and "Tethyan" ammonoid faunas as dependent on such factors as the water temperature. Investigation of recent squids (Zuev *et al.*, 1996) showed, however, that these cephalopods dwell in water, where the temperature is not lower than +19°C, and the optimal range for them is +22…+24°C. Judging from these data, the problem to divide cephalopods into "thermophilic" and "cryophilic" groups appears to be difficult. It is likely that we may speculate about the issue only in terms of "more or less thermophilic" taxa. Thus, the current subdivision of ammonoids into Boreal and Tethyan forms does not correspond to the present knowledge of their biogeography. In order to elucidate the possible biochore system, I qualitatively analyzed the generic and familial composition, outlined the diversification centers, and detected quantitative changes in ammonoid communities. This and other data now available allowed me to recognize five biochores, whose ammonoid assemblages are representative, have distinctive taxonomic compositions, and show specific degree of endemism at the generic level (the table). The known localities of ammonoids characterizing different evolutionary stages are shown in the geographical map (Fig. 2) and in a series of paleogeographic schemes for the Sakmarian, Artinskian, Kazanian (Wordian), and Tatarian (Dorashamian) ages, which are based on the topography reconstructed by Ziegler *et al.* (1996) from the University of Chicago.

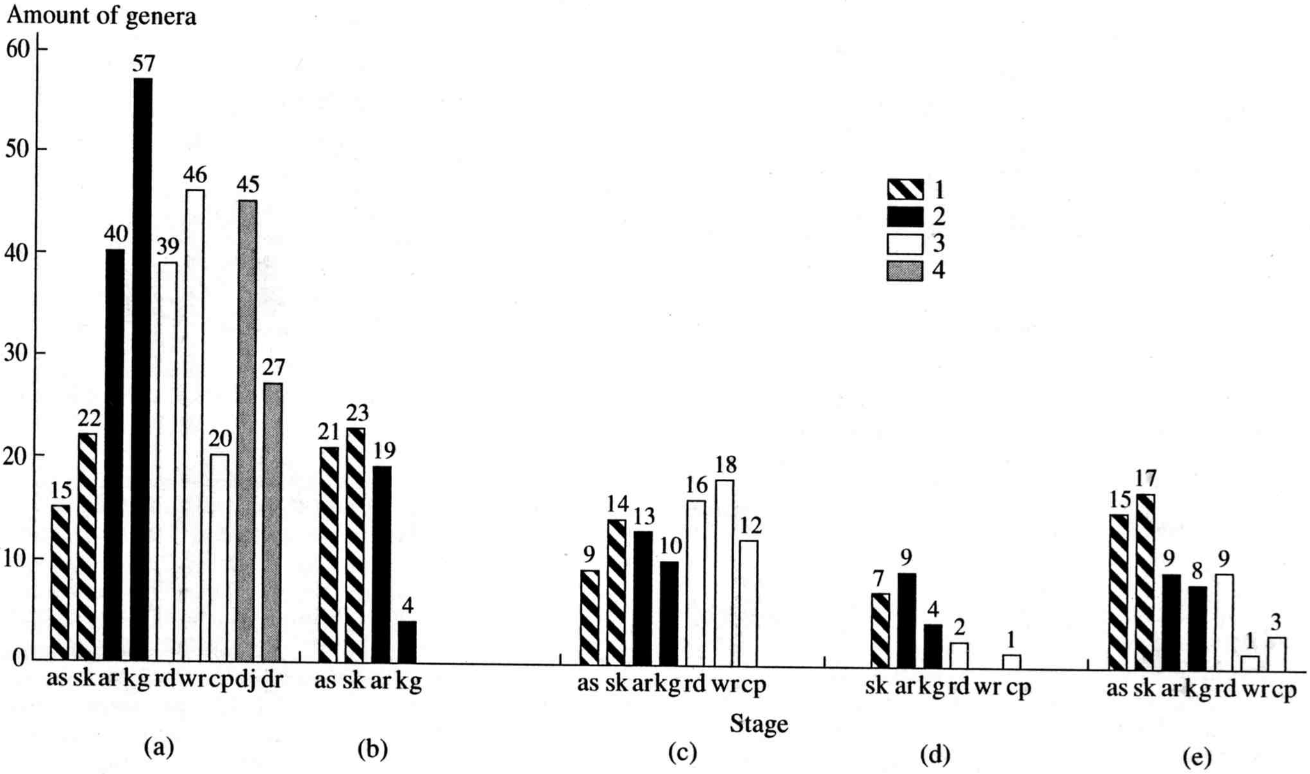

Fig. 3. Stage-related generic diversity of Permian ammonoids in various biogeographic areas: (1) first stage; (2) second stage; (3) third stage; (4) fourth stage; (a) Paleotethyan biochore; (b) Uralian biochore; (c) American biochore; (d) Arctic biochore; (e) Australian biochore. Stages: (as) Asselian; (sk) Sakmarian; (ar) Artinskian; (kg) Kungurian; (rd) Roadian; (wr) Wordian; (cp) Capitanian; (dj) Dzhulfian; (dr) Dorashamian (numbers above columns denote amount of genera).

PALEOTETHYAN BIOCHORE

The Paleotethys includes the ammonoid localities in Sicily, Crimea, Tunisia, Oman, Iraq (Kurdistan), Transcaucasia, Iran, Salt Range, Kashmir, Afghanistan, Pamirs, Darvaz, Tibet, China, Primor'e, Japan, Thailand, Malaysia, Timor, and Madagascar (Fig. 2). Most of ammonoid occurrences known at present are located in these regions, and they yielded the greatest number of Permian genera. The dynamics of generic diversity (Fig. 3a) is almost similar to that shown in the global scheme (Fig. 1).

At the first stage of the earliest Permian time (Fig. 4), 29 ammonoid genera known from the Paleotethys represented 45% of their total number, and only four of them were endemic (*Vanartinskia, Miklukhoceras, Parapronorites*, and *Martoceras*). Other genera were cosmopolitan, because this ocean, as mentioned above, was connected with the Uralian basins and also might have the fauna interchange with the American basins (indicative genera *Emilites* and *Properrinites*). According to available data, the Pamirs and Timor basins were the main diversification centers in the vast area of the Early Permian Paleotethys.

At the end of the Early Permian (second stage), more than 60 genera (or 80% of generic taxa of that time) inhabited the Paleotethys (Figs. 3a, 5). Nearly half of them, namely 28 genera were endemic. The late Artinskian–Kungurian ammonoid assemblages are the most representative as they include over 50 genera and 80 species of ammonoids. These were typical open-sea communities with abundant Medlicottiidae, Pronoritidae, Adrianitidae, and Perrinitidae. At that time, the basin of Pamirs was the largest diversification center, as it follows from the distribution analysis of medlicottiids (subfamily Sicanitinae, genera *Propinacoceras* and *Bamyaniceras* from subfamily Propinacoceratinae, and genus *Miklukhoceras*) and goniatites (family Perrinitidae; genera *Crimites, Veruzhites, Pseudoemilites*, and *Sosiocrimites* from family Adrianitidae; and also genera *Cardiella, Kargalites, Almites, Suakites*, and some others from the Marathonitidae family). Apparently, the geographic position of the Pamirs, between the eastern and western areas of the Paleotethys, was favorable, together with the free seaways for fauna interchange, for the origin and radiation of abundant new forms. The Timor and South China basins represented additional diversification centers inhabited by diverse and abundant ammonoid communities, where endemics represented a significant share of the population. Analysis of generic and specific composition of Artinskian and Kungurian ammonoids from the Pamirs, Darvaz, Afghanistan, southeastern China, Thailand, and Timor shows that there were persistent ways of fauna migration between these basins. Ammonoid assem-

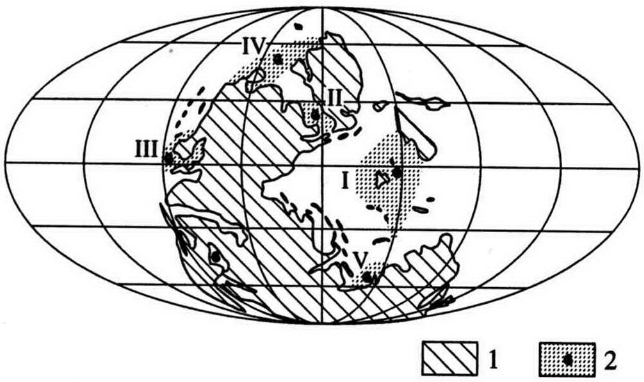

Fig. 4. Distribution areas of ammonoids at the beginning of the Early Permian (after Ziegler *et al.*, 1996, with additions): (1) land; (2) distribution areas of ammonoids; (I) Paleotethyan biochore; (II) Uralian biochore; (III) American biochore; (IV) Arctic biochore; (V) Australian biochore.

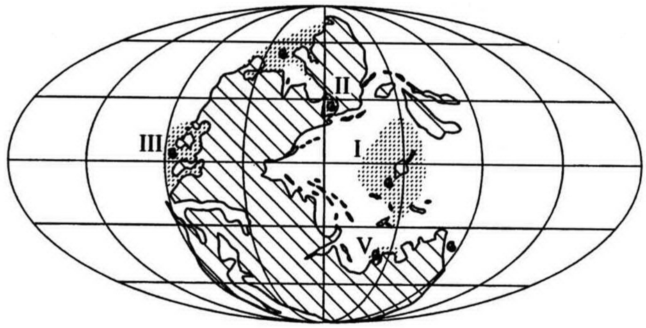

Fig. 5. Distribution areas of ammonoids at the end of the Early Permian (after Ziegler *et al.*, 1996, with additions; symbols as in Fig. 4).

blages from all these regions are rather similar in their taxonomic aspect, but they all show a high percentage of endemic forms. According to data on ammonoid distribution, basins of the Pamirs, Darvaz, and Afghanistan were situated near the South China block or between this structure and the Kimmerian epicontinent, but not as far away to the south and west from the southeastern China as is shown in palinspastic maps by McKerrow and Scotese (1990) or by Zonenshain *et al.* (1987). At any rate, there should be stable connections between the habitat areas of identical or close ammonoid communities. Investigation of present nautilus movement and distribution (Saunders and Spinosa, 1979) shows that the distribution areas of cephalopod species are not as great as was assumed in the concept of their free migration over the ocean. As it follows from observations, these areas have certain limitations and are not more than several hundreds kilometers across.

At the third stage of the early Late Permian (Fig. 6), the basins under consideration hosted 78–96% of all ammonoid genera, and 60–70% of this amount were represented by endemic taxa. At present, most representative distribution areas are known for the Wordian ammonoid faunas. Especially interesting are ammonoid assemblages from Sicily and the Timor. These two areas were situated in the extreme western (the former) and eastern (the latter) ends of a series of Wordian basins and likely represented the diversification centers from which many ammonoid forms migrated to meet one another. In this respect, the most spectacular examples are various Adrianitidae forms and close species from genera *Propinacoceras, Parapronorites*, and *Daraelites*. Between these centers, were located the basins of northern Iraq (Kurdistan), Oman, Tunisia, and Crimea, where abundant ammonoid communities consisted of identical or very similar species, and also the basins of Croatia and Chios Island (Greece), where their communities were less diverse. In the opinion of American experts (Bledinger *et al.*, 1992), there was also a seaway along the northern coast of Gondwana that connected the above areas and was favorable for the fauna interchange. To approve their idea, the cited researchers refer to data on coeval conodonts. The younger Amarassian ammonoids are known only from Timor Island, and this suggests that the formerly stable seaways were destroyed in the post-Wordian time.

Very diverse ammonoid assemblages of the initial Late Permian time are known from the basins of southeastern China. These assemblages are rich in endemic genera (over 50%), and the basins appear to have been partially isolated by certain barriers that provided the particular habitat environments for ammonoids. At the fourth stage of the terminal Permian time (Fig. 7), ammonoids survived in the Paleotethyan basins only (100%), as their remains are so far unknown from other localities. A series of these basins distinguished now in Transcaucasia, Iran, eastern and southeastern China, Far East, and Japan was populated by diverse and very peculiar ammonoid faunas. The Chinese scientist Zhou (1986) investigated in detail how the taxonomic composition of respective ammonoid communities depended on the type of their habitat basins. He demonstrated that the closed basins of the platform type and abnormal salinity accumulated in eastern and southeastern China the paralic coal-bearing deposits and were populated mostly by diverse ceratites, many of which were endemics and had the well-developed sculpture on shells peculiar in morphology. Several genera of goniatites (*Changhsingoceras, Pseudogastrioceras, Neoaganides*, and some others) and genus *Episageceras* of prolecanites were distinctly subordinate in these communities. Other ammonoid faunas very similar in taxonomic composition and general aspect are also known from the Upper Permian deposits of the Transcaucasia (Dzhulfa and Dorasham) and Iran (Abadeh). Sedimentation environments in all these

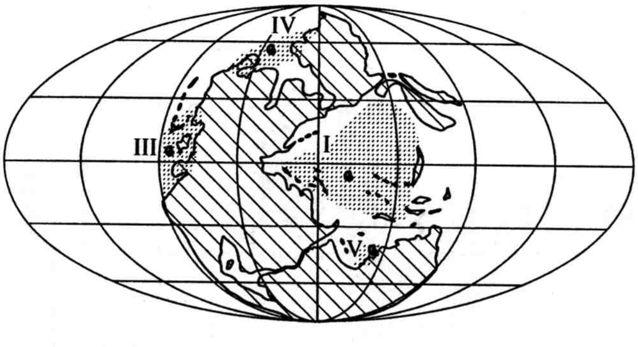

Fig. 6. Distribution areas of ammonoids at the beginning of the Late Permian (after Ziegler *et al.*, 1996, with additions; symbols as in Fig. 4).

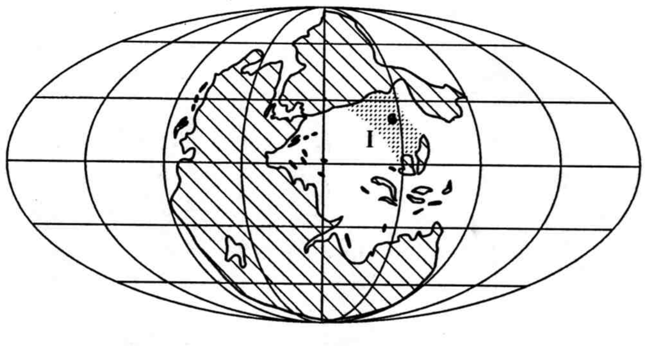

Fig. 7. Distribution areas of ammonoids at the beginning of the Late Permian (after Ziegler *et al.*, 1996, with additions; symbols as in Fig. 4).

areas were almost identical, and their shallow and closed epiplatform basins were interconnected through seaways suitable for migration of very specific ammonoids. The less representative ammonoid assemblages of the same type are described from the Kitakami area of Japan (Ehiro *et al.*, 1987, 1995) and from the Far East of Russia (Zakharov, 1994). It seems reasonable to take into account in all paleogeographic models that the regions of development of the Late Permian ammonoid fauna (Transcaucasia, Iran, South China, Japan, and the Far East) were located close to each other within a single biochore, being undivided by barriers impenetrable for these organisms.

URALIAN BIOCHORE

The Uralian biochore includes the ammonoid localities of central and southern Urals and of northern Kazakhstan (Fig. 2). In the basins of the Urals, ammonoids were especially diverse at the very beginning of the Permian (Asselian and Sakmarian ages), when they represented 64 and 59% of all coeval genera, respectively. Three families typical of the Permian (Paragastrioceratidae, Metalegoceratidae, and Popanoceratidae) and several new genera and species, which later became widespread in other Permian basins, originated in this biochore. Genera *Shikhanites, Neodimorphoceras, Protopopanoceras, Sakmarites*, and *Synuraloceras* are endemics and indicate that the Uralian biochore was the largest diversification center of the earliest Permian ammonoids. During the second stage, the relative diversity of ammonoids decreased, first to 34% (Artinskian Age) and then to 5.5% (Kungurian Age). The Artinskian Age was marked by a wide development of Paragastrioceratidae (genera *Paragastrioceras* and *Uraloceras*), which coexisted with diverse goniatites and prolecanites (endemic genera *Sakmarites, Aktubinskia*, and *Artioceras*). The Asselian and Sakmarian ammonoids are known mostly from southern areas of the Urals, whereas their Artinskian and Kungurian taxa are reported from more northern areas of the central Urals. Ammonoids postdating the Kungurian Age are unknown from the biochore in question (Fig. 3b).

AMERICAN BIOCHORE

The American biochore extends throughout Central and North America, except for Alaska, Yukon, and Arctic Archipelago of Canada (Fig. 2). During the Early Permian, ammonoids of the American biochore were moderately diverse and represented 27% of all Asselian and 36% of all Sakmarian genera. Four of the 23 genera that existed in this period were endemic (*Mescalites, Subperrinites, Leeites, and Nevadoceras*). At the second stage, the ammonoid diversity decreased to 23% in the Artinskian Age and to 14% in the Kungurian time, whereas the relative abundance of endemic genera (*Stenolobulites, Akmilleria, Metacrimites, Perrinites, Pseudovidrioceras*, and *Peritrochia*) became greater. The Early Permian genus *Stacheoceras* is known only from American regions. Since the very beginning of the Late Permian, the taxonomic diversity of ammonoid genera was growing to 32 and 38% in the Roadian and Wordian ages, respectively; in the Capitanian time, they already represented over 50% of all known genera. According to the preferable viewpoint, the La Colorado Formation of Mexico is of the late Capitanian age and corresponds to the Amarassian deposits in Timor bearing genera *Episageceras, Timorites, Kingoceras, Stacheoceras, Xenodiscus*, and *Eoaraxoceras* (Cantu-Chapa, 1997). Ammonoids of the fourth stage are absolutely unknown in the American regions (Fig. 3c). It should be mentioned, in addition, that the Wordian and Capitanian ammonoid assemblages from America are similar to those from the Paleotethys, but their direct interrelations remain ambiguous. Apparently, some other factors might be responsible for this circumstance.

ARCTIC BIOCHORE

The Arctic biochore includes the ammonoid localities of northeastern Asia, the Novaya Zemlya Archipelago, the Pai-Khoi Range, Vaigach Island, the Canadian

Distribution of ammonoid genera in various biochores

Stages	1					2					3					4				
Biochores / Ammonoid genera	Arctic	Uralian	American	Paleotethyan	Australian	Arctic	Uralian	American	Paleotethyan	Australian	Arctic	Uralian	American	Paleotethyan	Australian	Arctic	Uralian	American	Paleotethyan	Australian
Bulunites	■																			
Prouddenites	■																			
Parametalegoceras	■				■															
Neoglaphyrites	■	■																		
Preshumardites	■	■																		
Glaphyrites	■	■																		
Neodimorphoceras		■																		
Shikhanites		■																		
Synuraloceras		■																		
Protopopanoceras		■																		
Sakmarites		■					■													
Neoaganides		■												■						
Aristoceras		■																		
Mescalites			■																	
Leeites			■																	
Nevadoceras			■																	
Subperrinites			■																	
Vanartinskia			■	■																
Martoceras				■																
Daixites	■	■		■																
Tabantalites	■	■		■																
Properrinites	■		■	■																
Emilites	■		■	■																
Prothalassoceras	■	■	■	■																
Eoasianites	■	■	■	■																
Metapronorites	■	■	■	■																
Boesites	■	■	■	■																
Somoholites	■	■	■	■																
Juresanites	■	■		■	■															
Propopanoceras		■	■	■	■															
Svetlanoceras		■	■	■																
Neopronorites	■	■	■	■		■	■	■	■											
Uraloceras	■	■			■	■	■			■										
Paragastrioceras	■	■		■	■	■	■			■										
Artinskia	■	■		■			■													
Metalegoceras		■	■	■	■	■	■	■	■	■										
Crimites		■	■	■	■		■		■											
Almites		■	■	■			■		■											
Cardiella			■	■			■		■											

Table. (Contd.)

Stages	1					2					3					4				
Biochores / Ammonoid genera	Arctic	Uralian	American	Paleotethyan	Australian	Arctic	Uralian	American	Paleotethyan	Australian	Arctic	Uralian	American	Paleotethyan	Australian	Arctic	Uralian	American	Paleotethyan	Australian
Prostacheoceras		■	■	■					■											
Synartinskia		■		■					■											
Kargalites				■			■	■	■											
Miklukhoceras				■					■											
Akmilleria			■					■												
Stenolobulites			■					■												
Agathiceras	■	■	■	■	■			■	■	■			■	■	■					
Thalassoceras		■			■		■		■	■				■						
Medlicottia	■	■		■			■	■	■		■		■							
Propinacoceras				■			■		■				■	■						
Parapronorites				■					■					■						
Neouddenites						■														
Epijuresanites						■														
Gobioceras						■														
Neoshumardites						■	■													
Aktubinskia							■													
Artioceras							■													
Waagenina							■		■											
Neocrimites							■		■											
Metaperrinites								■	■											
Darvasiceras									■											
Paramedlicottia									■											
Prosicanites									■											
Eolegoceras									■											
Shyndoceras									■											
Perrimetanites									■											
Veruzhites									■											
Paraperrinites									■											
Pseudoemilites									■											
Pamiropopanoceras									■											
Artioceratoides									■											
Parasicanites									■											
Pamiritella									■											
Pamirioceras									■											
Pamirites									■											
Aksuites									■											
Suakites									■											
Istycoceras									■											
Zhonglopuceras									■											

Table. (Contd.)

Stages	1					2					3					4				
Ammonoid genera / Biochores	Arctic	Uralian	American	Paleotethyan	Australian	Arctic	Uralian	American	Paleotethyan	Australian	Arctic	Uralian	American	Paleotethyan	Australian	Arctic	Uralian	American	Paleotethyan	Australian
Pseudoshistoceras										■										
Tumaroceras						■					■									
Popanoceras						■	■	■	■	■	■			■	■					
Eothinites							■	■	■					■						
Daraelites							■	■	■					■						
Bamyaniceras								■	■	■			■	■	■					
Sosiocrimites								■	■				■	■						
Eumedlicottia								■	■				■	■						
Stacheoceras								■					■	■						
Perrinites								■					■							
Pseudovidrioceras								■					■							
Peritrochia								■												
Metacrimites								■												
Bransonoceras								■												
Aricoceras									■	■			■	■	■					
Hyattoceras									■				■	■						
Gaetanoceras									■					■						
Sicanites									■					■						
Eohyattoceras									■											
Lianyuanoceras									■					■						
Pseudohalorites									■					■						
Atsabites									■					■						
Mongoloceras											■									
Sverdrupites											■									
Daubichites											■				■					
Cyclolobus											■			■	■					
Neogeoceras											■			■						
Syrdenites											■			■						
Altudoceras											■		■	■						
Mexicoceras													■							
Kingoceras												■								
Glassoceras												■								
Texoceras												■								
Newellites												■								
Pseudagathiceras												■	■							
Tauroceras												■	■							
Paraceltites												■	■							
Demarezites												■	■							
Tongluceras												■	■							

Table. (Contd.)

Stages	1					2					3					4				
Ammonoid genera \ Biochores	Arctic	Uralian	American	Paleotethyan	Australian	Arctic	Uralian	American	Paleotethyan	Australian	Arctic	Uralian	American	Paleotethyan	Australian	Arctic	Uralian	American	Paleotethyan	Australian
Cibolites												■	■							
Waagenoceras												■	■							
Timorites												■	■							
Hoffmannia													■							
Palermites													■							
Adrianites													■							
Epadrianites													■							
Aristoceratoides													■							
Epithalassoceras													■							
Doryceras													■							
Shengoceras													■							
Paratongluceras													■							
Kufengoceras													■							
Liuzhouceras													■							
Epiglyphioceras													■							
Aulacaganides													■							
Lanceoloboceras													■							
Shaoyangoceras													■							
Angrenoceras													■							
Hengshanites													■							
Chekiangoceras													■							
Strigogoniatites													■							
Aulacogastrioceras													■							
Doulingoceras													■							
Guiyangoceras													■							
Elephantoceras													■							
Shangraoceras													■							
Sangzhites													■							
Erinoceras														■						
Paramexicoceras														■						
Roadoceras														■						
Jilingites														■						
Shuangyangites														■						
Shoushangoceras														■						
Yinoceras														■						
Epitauroceras														■						
Difunites														■						
Nodosageceras														■					■	
Episageceras														■					■	

Table. (Contd.)

Stages	1					2					3					4				
Ammonoid genera \ Biochores	Arctic	Uralian	American	Paleotethyan	Australian	Arctic	Uralian	American	Paleotethyan	Australian	Arctic	Uralian	American	Paleotethyan	Australian	Arctic	Uralian	American	Paleotethyan	Australian
Eoaraxoceras													■						■	
Xenodiscus													■						■	
Araxoceras																			■	
Rotaraxoceras																			■	
Prototoceras																			■	
Pseudotoceras																			■	
Vescotoceras																			■	
Urartoceras																			■	
Dzhulfoceras																			■	
Vedioceras																			■	
Avushoceras																			■	
Periptychoceras																			■	
Anfuceras																			■	
Konglingites																			■	
Jinjiangoceras																			■	
Qinglongites																			■	
Kiangsiceras																			■	
Sanyangites																			■	
Pericarinoceras																			■	
Pachyrotoceras																			■	
Xiangulingites																			■	
Lenticoceltites																			■	
Huananoceras																			■	
Pseudogastrioceras																			■	
Phisonites																			■	
Iranites																			■	
Dzhulfites																			■	
Shevyrevites																			■	
Paratirolites																			■	
Abichites																			■	
Changhsingoceras																			■	
Liuchengoceras																			■	
Rongjiangoceras																			■	
Pentagonoceras																			■	
Rotodiscoceras																			■	
Qianjiangoceras																			■	
Pleuronodoceras																			■	
Pernodoceras																			■	
Sinoceltites																			■	
Pachydiscoceras																			■	
Dushanoceras																			■	
Chaotianoceras																			■	
Pseudotirolites																			■	
Mingyuexiaceras																			■	
Pseudostephanites																			■	
Trigonogastrites																			■	
Tapashanites																			■	

Arctic Archipelago, Yukon, Alaska, and Greenland (Fig. 2). Ammonoids of this biochore were very diverse in the initial Early Permian time. Their genera represented 45% in the Asselian and 44% in the Sakmarian ages relative to the total number of coeval taxa. In addition to endemic genera *Bulunites* and *Prouddenites*, there were widespread species of *Paragastrioceras, Uraloceras, Prothalassoceras, Eoasianites, Metapronorites, Boesites, Somoholites, Juresanites*, and some other genera. Spinosa *et al.* (1991) reported on an interesting "intermediate" ammonoid fauna from Nevada and Yukon, where it is distinct due to the coexistence of "Boreal" genera *Paragastrioceras* and *Uraloceras* with the "Tethyan" genus *Properrinites* and cosmopolitan forms. The map illustrating distribution of the *Paragastrioceras–Uraloceras* fauna in this work should be supplemented with data on the localities of Sakmarian ammonoids in the Pamirs (Darvaz) and Australia. However, it is necessary to mention that two *Paragastrioceras* forms known from the Darvaz locality (Leven *et al.*, 1992) are scarce and small, suggesting a depressed state of this fauna in the last region.

At the second stage, the ammonoid fauna of the biochore became less diverse, and abundance of genera fell to 16% in the Artinskian and to 11% in the Kungurian ages. In contrast, the extent of endemism increased, and four genera (*Neouddenites, Epijuresanites, Tumaroceras*, and *Gobioceras*) of all ten existed in this period were endemics (table, Fig. 4).

The third stage marks the new event of diversity decrease, and the abundance rate of Roadian, Wordian, and Capitanian taxa became 18, 2, and 12%, respectively (Fig. 3d). The Roadian ammonoid assemblage includes only 9 genera, one of which (*Sverdrupites*) was endemic. The ammonoid assemblage from Greenland comprises the genus *Cyclolobus*, characteristic as well of the Paleotethys, and the geographic position of Greenland in the Permian time remains disputable.

AUSTRALIAN BIOCHORE

The biochore in question (Fig. 2) includes the ammonoid occurrences known in the Sakmarian–Capitanian sediments of western Australia and in the Artinskian–Roadian deposits in the eastern part of the continent. Their diversity changed in the following succession. During the first stage (Sakmarian Age), there were 8 genera (with a relative abundance rate of 18%), and almost all of them (*Agathiceras, Thalassoceras, Paragastrioceras, Uraloceras, Juresanites, Metalegoceras*, and *Propopanoceras*) were cosmopolitan. Nine genera of the second stage represented from 16% (Artinskian Age) to 5.5% (Kungurian Age) of the total amount of taxa. The widespread genera coexisted with *Pseudoshistoceras* forms characteristic of Australia only. The third stage with 6 genera (Fig. 3e) shows the following abundance rates: 4% for the Roadian, none for the Wordian, and 3% for the Capitanian. The ammonoid community under consideration was very enigmatic: *Agathiceras* and *Popanoceras* forms were cosmopolitan; genera *Bamyaniceras* and *Aricoceras* represented taxa simultaneously known from the Paleotethys; and *Daubichites* was a characteristic member of Boreal communities. In addition, the Capitanian deposits of western Australia yield *Cyclolobus* forms known as well from eastern Greenland, the Salt Range, Tibet, and Madagascar.

CONCLUSION

(1) The evolution history of Permian ammonoids can be divided into four principal stages: "pro-Permian" (initial Early Permian), "eo-Permian" (terminal Early Permian), "meso-Permian" (initial Late Permian), and "meta-Permian." Each of the stages included ammonoid assemblages displaying their own trend of biogeographic differentiation.

(2) Analysis of regional ammonoid faunas revealed five principal biochores: Paleotethyan, Uralian, American, Arctic, and Australian, each populated by communities with different dominant and endemic genera.

(3) Changes of the taxonomic diversity in the ammonoid biochores are as follows:

a) at the beginning of the Early Permian, the proportion of genera in common was rather high in all biochores;

b) the end of the Early Permian is marked by a distinct differentiation of the ammonoid distribution areas, though the Paleotethyan regions of Pamirs, Afghanistan, southwestern China, Thailand, and Timor were interconnected during the entire Early Permian period, and the fauna interchange was most intense in the second half of the period;

c) the free interchange of pelagic faunas at the commencement of the Late Permian (especially during the Wordian time) was typical of the basins of Sicily, Tunisia, Oman, Iraq, Crimea, Greece, Croatia, and Timor; the coeval ammonoid faunas of America also included many Paleotethyan forms;

d) at the end of the Permian, the shallow basins of southern China, Far East, Japan, Iran, and Transcaucasia were populated by affiliated ammonoid communities, probably because of similar habitat environments in the closely spaced basins interconnected by migration ways.

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