Reorganization of Marine Biota
during the Mid-Early Permian Epoch

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Abstract—The evolution history of fusulinids, brachiopods, ammonoids, and conodonts shows that while advancing across the Sakmarian–Artinskian boundary, all these faunal groups suffered a crisis that was followed by a peak of their speciation during the Kungurian (Bolorian) Stage. The regenerated Artinskian–Kungurian biota differs from that of the Asselian–Sakmarian time by a higher taxonomic diversity, and by the first appearance of the Late Permian elements. The critical moment coincides with a period of global regression, while the active development of rejuvenated biota and its expansion correspond to the transgression stage. The climatic changes were evidently another important factor, which affected the evolutionary trend of the studied fossils.

Key words: *fusulinids, brachiopods, ammonoids, conodonts, regression, transgression, Sakmarian Stage, Artinskian Stage, Yakhtashian Stage*

Recently, one of us (Leven, 1993a) recognized that the stages in fusulinid evolution are dependent on the transgressive-regressive cycles. Two first-order cycles were distinguished in the Permian history of the Tethys, and the Yakhtashian was determined as separating the regressive and transgressive regimes. Analyzing the cyclicity outside the Tethyan region, Leven (1994) concluded that it is of a global rank, and should consequently influence not only the fusulinid evolution, but also other groups of fossils. The present study is devoted specifically to this issue. In addition to fusulinids, we analyzed pertinent stages in the evolution of brachiopods, ammonoids, and conodonts using data, which characterize not only Tethys, but other basins as well—specifically, those of East European and North American provinces.

Inasmuch as the tracing of geological events in vast areas is highly dependent on the precision of stratigraphic correlation between sections which recorded these events, we must first consider data on the critical point between the regressive and transgressive phases distinguishable in the above regions (Fig. 1). In the Tethyan region, it corresponds to the Yakhtashian Stage. The Sakmarian and tightly related Asselian deposits always occur here below the unconformity. The rocks above it are most often of the Bolorian age. Less frequently, they correspond to the Kubergandian Stage, and sometimes the basal beds of the transgressive sequence can be considered (with minor reservations) as late Yakhtashian in age.

The Yakhtashian Stage of the Tethyan scale is usually thought to be correlative with the Artinskian Stage. This is based on finds of the late Artinskian ammonoids yielded by the uppermost Yakhtashian horizons in the stratotype section of the latter stage (Leven *et al.*, 1992), and on the Artinskian conodont and ammonoids occurring together with the Yakhtashian fusulinids (*Pamirina, Darvasites*, and *Chalaroschwagerina vulgaris*) in some sections of southern China (Zhang Lixin *et al.*, 1988; Zhou Zuren, 1989). However in the Puan sections, the early Artinskian ammonoids associate with fusulinids (*Sphaeroschwagerina glomerosa* and *Rugosofusulina*), which are more archaic as compared to the Yakhtashian forms. Consequently, the lower boundaries of the Yakhtashian and Artinskian stages can be discordant, the former corresponding to a higher level. In this case, the Yakhtashian Stage would approximately correspond to the upper Artinskian substage of the Uralian scale. Then, in terms of standard scale units, the regression in the Tethyan regions can be referred to the middle of the Artinskian Stage, and the initiation of the late Yakhtashian transgression can be dated as the terminal event of this stage. The Uralian sections indirectly support this conclusion as well, because basal fine-clastic rocks of the Artinskian Stage are replaced here upward by coarse pebble-boulder deposits of its middle unit (the Irgina and Sarga horizons), which indicates a general uprising and basin shoaling. This regressive trend is swapped at a higher level by a transgressive clay-carbonate sequence of the Sarana Horizon, the terminal one in the Artinskian Stage (Chuvashov *et al.*, 1990).

	North America		Urals		Tethys		Northeast Russia
		Roadian Stage	Ufimian Stage		Kubergandian Stage		Omolon Horizon
	Leonardian / Formation	Cathedral Mountains Fm.	Kungurian Stage		Bolorian Stage		Djigdaly Horizon
		Skinner Ranch Fm.	Artinskian Stage		Yakhtashian Stage		
Stage	Wolfcampian / Formation	Lenox Hills Fm.	Sakmarian Stage		Sakmarian Stage		Munugudjak Horizon
		Neal Ranch Fm.	Asselian Stage		Asselian Stage		

[·····] 1   [▲▲▲] 2   [----] 3

Fig. 1. Correlation between different stratigraphic scales of the Lower Permian (1, ammonoids; 2, conodonts; 3, fusulinids).

In sections of northeastern Asia, the critical level separating the cycles corresponds to the boundary between the Munugudjak and Djigdaly horizons, correlative with the middle Artinskian substage. This is evident from the fact that an upper part of the Djigdaly Horizon yielded early Artinskian (*Neoshumardites triceps* Ruzh.) and Kungurian (*Neouddenites, Daraelites*, and *Epijuresanites*) fossils (Ganelin, 1984; Ganelin *et al.*, 1990). The transgressive sequence of the North Pechora zone begins with the Gusinaya and Bel'kovskaya formations of the late Artinskian age (Bogomazov *et al.*, 1984). In Spitsbergen, a larger part of the Artinskian Stage is composed of gypsum-bearing deposits. The Kapp Starostin Formation transgressively overlying this deposits yielded conodonts of the transitional Artinskian–Kungurian age (Szaniawski and Malkowski, 1979). In the Canadian Arctic, margins of the Sverdrup basin suffered uprising movements during the second half of the Artinskian Stage (the Melvillian disturbance); the next stage of subsidence was at the very end of the Artinskian, or during the Kungurian Stage (Beauchamp, 1993).

In the Mid-Continent basin of North America, both events under consideration left behind a remarkable surface of unconformity, separating the Wolfcampian and Leonardian series. The first of them is subdivided into the Neal Ranch and Lenox Hills formations of the Glass Mountains. The uppermost horizons of the latter yielded the lower Artinskian assemblage of conodonts. In basal beds of the Leonardian Series (the Skinner Ranch Formation above the unconformity), this group of fossils is of the late Artinskian age (Movshovich *et al.*, 1979; Ritter, 1986). Data on conodonts are somewhat discordant relative to the data on ammonoids from the Lenox Hills Formation, according to which, the latter is of the Sakmarian age.

Sakmarian ammonoids were also discovered in the Hueco Formation of the same mountains (Williams, 1963). The overlying Cerro Alto Formation corresponds to a greater part of the Lenox Hills Formation in the Glass Mountains (Williams, 1963; Ross, 1963). This favors the viewpoint of Furnish (1973), who suggested the Sakmarian age of the latter. Thus, the data above need to be better correlated.

Summarizing all the information, we may state that in the principal basins of the Permian marine sedimentation, the transition from the regressive to transgressive stage was nearly synchronous worldwide, and corresponded to the second half of the Artinskian Stage and the initial interval of the Kungurian Stage. The regression maximum is confined to the middle Artinskian interval, or, when estimated more precisely, to the first half of this stage. Despite some discrepancy of dating, it is clear that the geological events under discussion were of a global rank, and therefore, should influence marine biota evolution everywhere. The faunal groups under analysis, i.e., the benthic fusulinids and brachiopods coupled with pelagic ammonoids and conodonts, were the most abundant in the Permian seas, and their evolutionary trends during the mid-Early Permian should conventionally reflect the evolution of marine biota in gross.

FUSULINIDS

This well studied group of very abundant and widespread marine fossils of the Late Paleozoic is a perfect object to study the character, scale, and dynamics of biotic changes during the selected interval of geological history. However, it is difficult to analyze fusulinid evolution as a whole, because they show individual evolutionary patterns in different biochores and a provincial character of distribution. Therefore, we consider this problem below, using the principal Permian biochores as examples.

Tethys. Fusulinids in this basin were very abundant and taxonomically diverse. As it was earlier demonstrated by Leven (1993a, 1993b, 1994), their communities suffered significant changes passing across the

Sakmarian–Yakhtashian boundary. These changes were as follows:

(1) The species composition was completely rejuvenated.

(2) Alternation of dominants was typical at both the generic and specific levels. Characteristic Asselian and Sakmarian representatives, such as genera *Sphaeroschwagerina, Pseudoschwagerina, Paraschwagerina, Zellia, Rugosofusulina, Dutkevitchia,* and *Quasifusulina* became extinct, or considerably limited in abundance. Dominant taxa were genera *Chalaroschwagerina* and *Praeskinnerella,* which appeared for the first time, *Darvasites,* which existed earlier, and new species of pseudofusulines, such as *Pseudofusulina kraffti, P. fusiformis,* and some other forms.

(3) Several newborn genera (*Pamirina, Mesoschubertella,* and *Toriyamaia*) were taxa characterizing only the second half of the Early Permian.

(4) Some new genera, which appeared during the Yakhtashian and Bolorian stages, became ancestors of higher taxa prosperous later, during the Late Permian. These were: *Misellina,* the first genus of the order Neoschwagerinida; *Yangchienia,* representing the monotaxonic family Yangchienidae, and such genera as *Nankinella* and *Staffella,* both ancestral in the Nankinellidae and Staffellidae families.

(5) The most prominent changes in Early Permian fusulinid assemblages were recorded in the southern peri-Gondwanan part of the Tethys, where the endemic Sakmarian complex of relatively cryophilic species was replaced by typical thermophilic forms (Leven, 1993b).

The dynamics of Tethyan fusulinid evolution is illustrated by a series of histograms (Fig. 2) showing variations in the amount of genera during the Early Permian. As one can see in the first histogram, the Sakmarian–Yakhtashian boundary marks the peak extinction of older genera associated with the maximum of newborn taxa, the latter promoting general growth of their abundance.

Other histograms (Fig. 2, parts 2 and 3) well illustrate the rejuvenation degree of fusulinid assemblages. The first shows the percentage of newborn genera relative to their total number during a particular time interval. It is clear that the rejuvenation peak (59%) was dur-

ing the Yakhtashian Stage. For comparison, respective values are 48% for the Carboniferous–Permian, and 40% for the Early–Middle Permian boundary intervals. Ratios of newborn genera to their total amount at the preceding stage are even more indicative: 75% for the Yakhtashian Stage, and only 60% for the Asselian and 50% for the Kubergandian stages. The last histogram (Fig. 2, part 3) illustrates percentage ratios between the genera extinct before the upper boundary of a stage and all the genera that existed at this stage. Here, one can easily see that fusulinids suffered two significant crises during the Early Permian—first, at the end of the Sakmarian Stage (40% of genera), and next, at the end of the Bolorian Stage (45% of genera).

Boreal regions. Connections between the Boreal and Tethyan provinces were either interrupted, or irregular since the Sakmarian time. These discriminated fusulinid assemblages inhabited respective basins. As compared to the Tethyan communities, the Sakmarian and Artinskian fusulinids from the Arctic regions of Canada, Spitsbergen, the Urals and the Timan-Pechora area are distinctly less diverse. Representatives of the genus *Pseudofusulina* are obviously dominant among them, and associate with few other genera of low specific diversity.

In East European basins, the post-Sakmarian regression did not result in a complete drying of the region, but it caused a more intense supply of the basin with coarser sedimentary material (especially during the middle Artinskian time) derived from the Uralian uplifts. Accordingly, biotic changes during the period under discussion were evident here, but not as prominent as in the Tethys. For instance, Chuvashov (1984) reported that fusulinids from the Burtsevka Horizon of the Artinskian Stage resemble those from the Sterlitamak Horizon of the late Sakmarian age. Using these data, he suggested to discriminate an independent Yuresan' regiostage comprising the two units mentioned above and the Irgina Horizon overlying them. Such a new stage seems to be very conventional, because the Irgina time marks an important moment in fusulinid evolution, when the first occurrence level of their elongated forms with cuniculi (*Praeparafusulina lutugini*) were soon replaced up-section by parafusulines. It should be noted that in the Tethyan
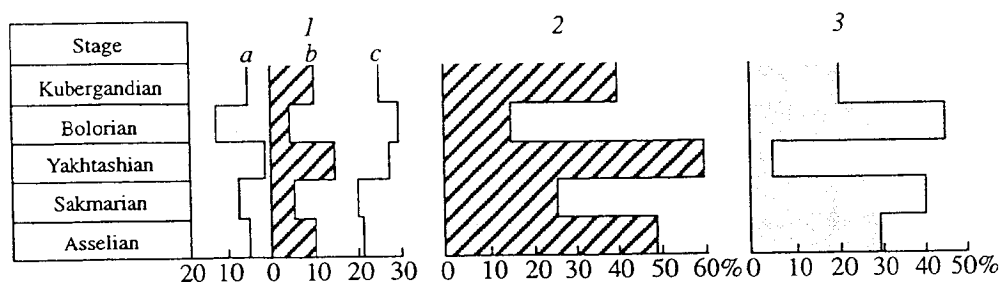

Fig. 2. Fusulinids: histogram demonstrating secular variations (*1*) in distribution of extinct (*a*), new (*b*), and all (*c*) fusulinid genera; percentage of new (2) and extinct (3) genera relative to their total amount at different stages.

regions, the first cuniculi in fusulinid forms appeared at the end of the Yakhtashian–Bolorian interval, and, according to Bogoslovskaya (1988), the Irgina assemblage of fusulinids is of the late Artinskian age, though in standard stratigraphic schemes of the Urals the Irgina Horizon it is still assigned to the early Artinskian substage.

In other Boreal basins, which were inhabited by Early Permian fusulinids (from Alaska on the west to Spitsbergen on the east), the middle Artinskian events resulted in the complete extinction of this faunal group. There are many reasons to believe that this was a consequence of regression, which left respective marks in many sections of Canada and Spitsbergen. Fusulinids of the Asselian, Sakmarian, and Artinskian age (up to the Irgina and possibly Sarga horizons) occur mostly in the carbonate Belcher Channel Formation of the Sverdrup basin. The basal third of the overlying Assistance Formation (and its analogs) contains the Roadian (=Kubergandian, or Ufimian) fusulinids, as well as conodonts. According to Kozur (1977), the latter group corresponds to the Bolorian conodonts of the southeastern Pamirs. Some researches (Nassichuk, 1975; Nassichuk and Wilde, 1977) noted a hiatus below the base of the Assistance Formation, and Chuvashov (1984) considered this hiatus as comprising the entire Artinskian Stage, the latter corresponding, in his opinion, to a stratigraphic range from the Sarga Horizon to the upper boundary of the Kungurian Stage. If we take into account conodonts, which are Bolorian (=Kungurian) in age and occur at a higher level than the base of the Assistance Formation (Kozur, 1977), then the initial level of the hiatus should be assigned to the second half of the Artinskian, or possibly, to the very beginning of the Kungurian time. A similar conclusion is inferable from data on Spitsbergen, where the Wordiekammen Limestone contains the Sakmarian (not younger) fusulinids (Ross, 1963). The gypsum-bearing deposits above this unit seem to correspond to the regression stage. The overlying basal part of the Kapp Starostin Formation yielded conodonts of the transitional Artinskian–Kungurian age (Kozur, 1978), marking the initial transgression. Paleogeographic, paleoclimatic, and paleoecologic transformations, i.e., all the results of the Artinskian regression in the Boreal province, were significant to such an extent that fusulinids were unable to survive them, and all over the province, the Upper Permian deposits are barren of these fossils.

North American regions. The Permian type sections of the Mid-Continent basin show that most significant changes in fusulinid assemblages were at the Wolfcampian–Leonardian boundary, which is often confined to a surface of unconformity. Here, similar to the Tethyan regions, fusulinid assemblages of the Asselian and Sakmarian (possibly Sakmarian–early Artinskian) stages, respectively correlative to the Neal Ranch and Lenox Hills formations, display many common features. Both assemblages include loosely spiraling forms, such as *Pseudoschwagerina* and *Paraschwagerina*. These forms disappear above the unconformity in the Skinner Ranch Formation, where dominant species correspond to highly developed representatives of the genera *Pseudofusulina, Skinnerella,* and *Parafusulina,* most prosperous during the Late Permian. The difference between the assemblages is very sharp, suggesting a significant hiatus in sedimentation separating the accumulation periods of respective host deposits. This was first noted by Ross (1963), who concluded that *Chalaroschwagerina nelsoni* and *Pseudoschwagerina gerontica* beds, distinguishable in an upper part of the Alacran Mountain Formation (the Hueco region), are missing in sections of the Glass Mountains.

BRACHIOPODS

Like fusulinids, brachiopods are benthic organisms with a highly provincial distribution. Therefore, their evolution could also be traced in separate large biochores.

Tethys. The most distinct critical point in the Tethyan brachiopod evolution is related to the Yakhtashian regression. It was of particular significance in the peri-Gondwana regions (Iran, Arabian Peninsula, southern Afghanistan, southern Pamirs, Karakorum, Himalayas, northern India, southern Tibet, and Australia), where the biotic impact during regression and subsequent transgression was significantly magnified by climatic factors. Here, the late Asselian (?)–Sakmarian communities of brachiopods generally consisted of cryophilic forms of the so-called Gondwanan type. They included approximately 20 genera, among which *Taeniothaerus, Punctocyrtella, Notospirifer,* and *Triginitreta* were the most indicative (Grunt and Dmitriev, 1973; Grunt, 1993; Archbold and Gaetani, 1993). In many of these regions, the Yakhtashian interval corresponds to a hiatus in sedimentation, and the features of respective brachiopod assemblages are unclear.

The Bolorian brachiopods are abundant in the southeastern Pamirs (Grunt and Dmitriev, 1973) and Khao Phric locality of southern Thailand (Grant, 1976). They are very different in taxonomic composition from the Sakmarian community. Only one genus is inherited from the latter, while the species list includes absolutely new forms. The much more diverse Bolorian community comprises over 70 genera, including 30 endemic taxa such as *Incisicus, Transennatia, Bibatiola, Celebetes, Haydenella, Posicomta, Cryptospirifer, Spirigerella, Boloria, Overtoniina, Uncinella,* and others. Many of them became widespread in the Late Permian basins of the Tethys. Other genera were of a wider stratigraphic and geographic distribution. It is remarkable that some genera of the latter type also occur below the Bolorian deposits in the northern Tethyan regions, as well as in the southern Urals, which was a part of the tropical climatic zone during the Asselian–Sakmarian time. This suggests that reorganizations in the peri-Gondwanan brachiopod assemblages resulted not only from ecological changes during the Yakhtash-

ian regression, but also from the migration of their thermophilic forms into the southern Tethyan regions. The latter was possible because of the climatic warming of the Yakhtashian time.

The above analysis of fusulinid assemblages implies the same conclusion. In general, the Bolorian brachiopods from the southern Tethys do not display evolutionary links with older Sakmarian forms, thus representing an absolutely new assemblage consisting of endemics and migrants from warm-water basins. The initial formation of the assemblage is likely rooted in the Yakhtashian Stage, when most respective innovations were not a consequence of evolutionary transformations, but rather, a result of the arrival of thermophilic migrants superseding cryophilic forms.

In the northern Tethyan regions, i.e., in equatorial basins of the Early Permian time, climatic factors were insignificant, and the changes in brachiopod assemblages were of a different character. According to our data on southwestern Darvaz, the late Asselian–early Sakmarian brachiopods represented, as in the southern Urals, significantly diverse reef assemblages there. Many of their genera, such as *Enteletes, Chaoiella, Tubaria, Keyserlingina, Echinoconchus, Urushtenia, Trautsholdia, Brachythyrina, Choristites, Crurithyris, Eliva, Wellerella, Stenoscisma,* and others, are similar to Uralian taxa. Nevertheless, they usually include endemic species.

In Darvaz, the upper Sakmarian and lower Yakhtashian deposits belong to terrigenous facies nearly always barren of brachiopods. These fossils appear higher in the section, at the level of the Safetdaron Formation corresponding mostly to the Bolorian Stage. In general, brachiopods from this formation are characteristic of the reef assemblages, and resemble late Asselian–Sakmarian forms. At the same time, this is the first occurrence level of many genera and species recorded in the Bolorian deposits of the southern Tethys, for instance, in the Khao Phric locality. Such features may point to a low climatic gradient between the peri-Gondwanan and equatorial regions of the Tethys.

East European basins. Despite a somewhat impoverished taxonomic composition, the Sakmarian brachiopods from these basins are closely related to the Asselian forms. In both groups, many taxa are inherited from the Middle–Late Carboniferous biota. Their characteristic representatives are the following genera: *Enteletes, Meekella, Kozlowskia, Chaoiella, Reticulatia, Tubaria, Retaria, Marginifera, Keyserlingina, Echinoconchus, Urushtenia, Callispirina, Rugivestis, Juresania, Trautsholdia, Brachythyrina, Choristites, Purdonella, Crurithyris, Eliva, Tiramnia, Federicksia, Punctospirifer, Wellerella, Stenoscisma,* and *Leiorhynchus.* These genera are typical of thermophilic communities, and in addition to bryozoan and algae, they contributed much to the formation of reef structures such as the Shikhan and Sterlitamak reefs. Many of the

above genera became extinct before the end of the Sakmarian Stage. During the Asselian and Sakmarian stages, the latter in particular, these genera were associated with rare representatives of taxa, which later became important constituents of brachiopod assemblages. To exemplify such taxa, we may list genera *Chonetina, Dyoros, Arctochonetes, Kochipr luctus, Achunoproductus, Jakovlevia, Anidanthus, Muirwoodia, Megousia, Waagenoconcha, Neospirifer,* and *Spiriferella.*

Though significantly impoverished, the early Artinskian (Burtsevka Horizon) brachiopod assemblages are still similar to their Sakmarian counterparts. The r rejuvenation was initiated at the late Artinskian level, and resulted in a much higher taxonomic diversity. For instance, the Sarga Horizon yielded 140 brachiopod species of 55 genera. This faunal group is enriched in chonetids (*Quadrochonetes, Dyoros, Chonetina, Tornquistia, Svalbardia, Arctochonetes,* and *Neochonetes*), spiriferids (*Cyrtella, Spiriferella, Neospirifer,* and *Torynifer*), and productids (*Megousia, Thuleproductus, Jakovlevia, Uraloproductus, Horridonia, Sowerbina, Anemonaria, Avonia,* and *Paucinispinifera*). They associate with widespread rhynchonellids (*Rhynchopora*) and terebratulids (*Dielasma* and *Beecheria*). In contrast to pre-Artinskian brachiopods, which clearly represent thermophilic communities typical of the northern Tethys, the late Artinskian assemblages included more cryophilic forms characteristic of the West Arctic basins of the Late Permian. Respectively, forms of the Tethyan type gradually became less abundant, reflecting the progressing isolation of the East European basins from the Tethys and an expansion of the Boreal fauna.

The Kungurian regression was unfavorable for the brachiopod evolution, and their assemblages from that time are less abundant and diverse than the Artinskian taxa. The Timan–Pechora region was the only exception, and the brachiopod communities here underwent the next rejuvenation stage, evolving further under preserved marine conditions.

Taimyr–Kolyma basins. Changes in brachiopod communities represent only one aspect of general ecological transformations—those which affected these regions during the mid-Artinskian time. This level marks the boundary between two large cycles of sedimentation (Kashik *et al.,* 1990), and a critical point when fauna of one ecological type was replaced by another. At this very moment, older faunal groups of the Verkhoyansk type were replaced by extremely different fauna of the Djigdaly type. This general reorganization is evident in all biotic groups (Ganelin and Kotlyar, 1984a, 1984b).

Changes in brachiopod assemblages are the most thoroughly studied. The Asselian–early Artinskian brachiopod communities included eight families of Rugosochonetidae, Anopliidae, Overtoniidae, Linoproductidae, Rhynchoporidae, Neospiriferidae, Elithidae,

Amboco idae, and Pugnacidae. Three of them (Ano-
pliidae,   rtoniidae, and Pugnacidae) totally disap-
peared fr   the basins of northeastern Asia at the strati-
graphic   el under discussion. Seven other families,
including uch important groups as Meekellidae, Bux-
toniidae. iorridoniidae, and Licharewiidae, appeared to
replace them. Changes at the generic level were equally
essential. For instance, as many as nine genera disap-
peared from the assemblage of 16 genera typical of the
Munugudjak Horizon, among them such taxa as *Torn-
quistia* nd *Jakutoproductus*, previously dominant
among   e others. New taxa of the Djigdaly time
include early 20 genera, among which *Meekella, Lis-
sochonetes, Waagenoconcha, Sowerbina, Megousia,
Pseudosvringothyris, Tumarinia, Timaniella, Alispir-
iferella, Crassispirifer*, and *Tomiopsis* were the most
abundant. One more feature is a higher diversity at the
specific level (up to 45 species, nearly all rejuvenated).

It is important that outside the region, for instance in
the East European basins, many genera and species of
the Djigdaly Horizon occur in older deposits as well.
Their appearance in northeastern Asia shows that the
Djigdaly transgression and related lowering of climatic
gradients were favorable for distant migrants. From this
moment on, the biota of northeastern Asia was acquir-
ing features common to the coeval faunas of the main
Arctic basins to finally become considerably less
endemic than before.

North American regions. During the Early Permian,
the Mid-Continent basin was in the tropical zone, and
accordingly, the transition from Sakmarian to subse-
quent brachiopod assemblages was more gradual here
than in the southern Tethys. In addition, the post-Sak-
marian regression was short and not very sharp in this
area. Nevertheless, like everywhere else, the Artinskian
Stage was critical for the brachiopod evolution even
here. Their remains are studied most thoroughly in the
Glass Mountains (Cooper and Grant, 1972). A series of
new forms was discovered in this locality from the
Skinner Ranch Formation, which is correlative to the
Artinskian Stage of the Urals according to ammonoids,
or to its upper substage according to conodonts. The
first occurrence level for such genera as *Acolosia,
Chonosteges, Coscinophora, Cyclacantharia, Entr-
onaria, Cartorhium, Oncosarina, Rhamnaria, Rug-
aria*, and *Thamnosia*, is at the formation base. The first

specimens of the *Paranorella* genus were recorded in
its middle part, while the upper part yielded representa-
tives of *Sceletonia, Torynechus, Gliptosteges, Lepidos-
pirifer, Phrenophoria, Plectelasma, Elassonia*, and
Tschernyschewia genera. Many of the listed genera
occur only in the Skinner Ranch Formation, though
some of them are also widespread in the overlying
Cathedral Mountain Formation.

Despite the fact that brachiopods from the Skinner
Ranch Formation are enriched in new forms absent in
the older Lenox Hills Formation, both formations are
closely interrelated and contain many common genera,
such as *Scachinella, Derbyia, Eolyttonia, Geyerella,
Kochiproductus*, and some others. Cooper and Grant
considered distribution of this kind to be important
enough to refer the Skinner Ranch Formation to the
Wolfcampian Group. However, it seems to be more cor-
rect to detect stratigraphic levels on the basis of newly
appeared taxa, especially when such changes are also
typical of coexisting fusulinids and ammonoids, which
are even more pronounced among the two latter groups.
Upsection of the Skinner Ranch Formation, most of its
older Wolfcampian elements of fauna disappear, and
brachiopod assemblages from the Cathedral Mountain
Formation are absolutely rejuvenated in comparison
with those from the Lenox Hills Formation.

AMMONOIDS

Pelagic ammonoids are more cosmopolitan as com-
pared to fusulinids and brachiopods. The principal fea-
tures of their evolution were similar in different basins.
Formed at the beginning of the Early Permian, this fau-
nal group persistently evolved toward greater taxo-
nomic diversity up to the end of the Bolorian Stage,
when the most characteristic taxa of the Early Permian
time underwent a global extinction. The general course
of evolution was not very regular, as is evident from the
histograms in Fig. 3. They show that the initially
smooth diversification of ammonoid genera was dis-
turbed by a speciation outbreak during the Artinskian
Stage. This outbreak was preceded by an extinction
event of the terminal Sakmarian time, which was the
most significant for the entire Early Permian interval.
Changes at the Sakmarian–Artinskian boundary simul-
taneously modified the abundance and diversity of
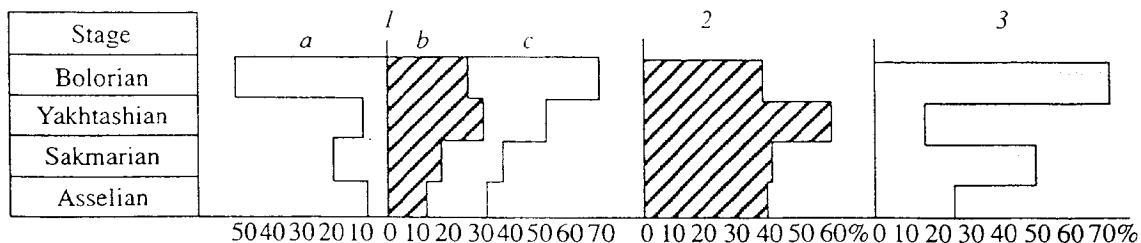ammonoids. Many genera of Carboniferous origin,

Stage
Bolorian
Yakhtashian
Sakmarian
Asselian

50 40 30 20 10 0 10 20 30 40 50 60 70   0 10 20 30 40 50 60% 0 10 20 30 40 50 60 70%

Fig. 3. Ammonoids: histograms demonstrating secular variations (*1*) in distribution of extinct (*a*), new (*b*), and all (*c*) fusulinid gen-
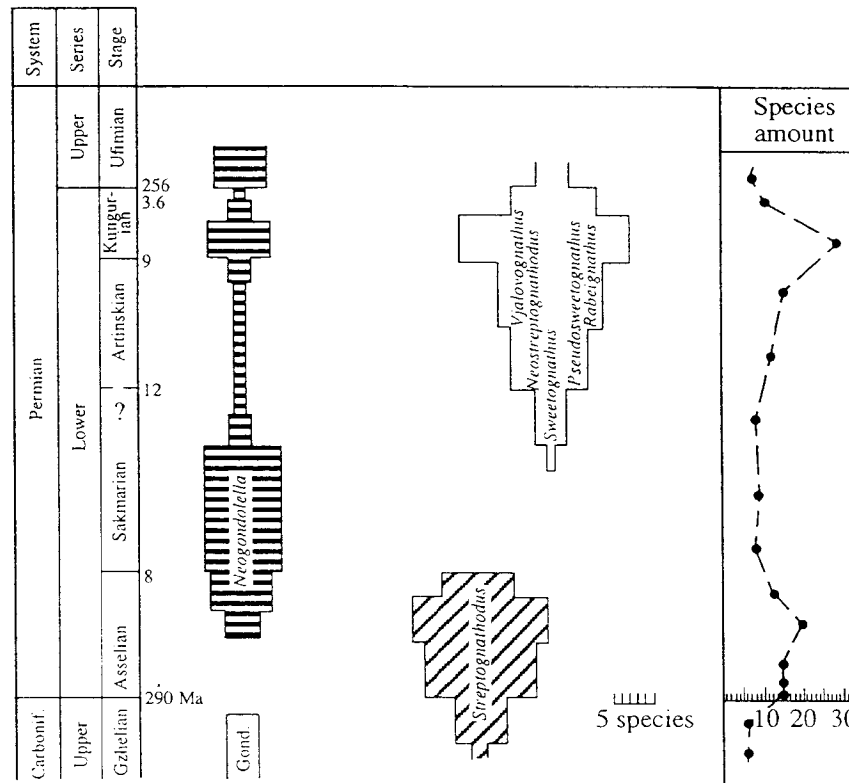era; percentage of new (*2*) and extinct (*3*) genera relative to their total amount at different stages.

Fig. 4. Species diversity of main Early Permian conodont genera.

which were widespread during the initial interval of the Early Permian, ceased to live during the Sakmarian Stage. These were *Boesites, Metapronorites, Eoasianites, Glaphyrites, Somoholites,* and *Emilites.* Only four long-lived genera (*Neopronorites, Artinskia, Neoaganides,* and *Agathiceras*) survived this stage to become significant components of subsequent ammonoid biota. The beginning of the Artinskian Stage was the first occurrence level for *Daraelites, Eothinites, Popanoceras, Waagenina,* and *Perrinites* genera, the taxa characteristic of the entire second interval of the Early Permian. Simultaneously born genera *Aktubinskia, Artioceras,* and *Neoshumardites* were of a lesser vitality, and died at the end of the Artinskian Stage. All listed genera indicating the commencement of this stage initially had a very limited distribution and abundance like other ammonoid assemblages of that time. The only exception was the biota of the southern Urals (Ruzhentsev, 1956), which included very abundant and diverse ammonoids of the early Artinskian age (Burtsevka and Aktasta horizons). Their intense speciation was confined to the mid-Artinskian time (Bogoslovskaya, 1988). The well-known and rich Artinskian fauna of ammonoids attained its final complexion precisely at this moment. The Urals and Tethys were principal areas of its origin, diversification, and distribution.

An intense speciation and expansion of ammonoid fauna during the mid-Artinskian time continued through the Bolorian (Kungurian) Stage, when over 20 new genera appeared in ammonoid communities (Andrianov, 1985; Leonova and Dmitriev, 1989; Leven *et al.,* 1992). However, many of these genera were limited in distribution by their source regions.

The late Bolorian (late Kungurian) crisis marked the terminal moment in the history of the Early Permian ammonoids, because nearly all their genera of that period ceased to live, regardless of the time of their origin, and completely disappeared. After the mass ammonoid extinction at the Bolorian–Kubergandian boundary, paraceltites (the Permian ceratites) and goniatites with the most complex septa (Kufengoceratidae and Cyclolobidae) were the main *personages* of the Permian history of ammonoids.

Thus, the mid-Early Permian event at the Sakmarian–Artinskian boundary was the principal one in the history of ammonoid fauna, and resulted in cardinal biotic changes which influenced its further evolution. This event subdivided the history into two large intervals with similar evolutionary trends. The short initial period of each interval was the phase of biota formation (the initial phase of the Asselian Stage and the Burtsevka time of the Artinskian Stage), when ammonoid groups were small and included many older forms. These were also the origin phases for large taxa, whose rapidly evolving representatives created the basis of subsequent biotas. Such taxa included four families (Paragastrioceratidae, Metalegoceratidae, Perrinitidae, and Popanoceratidae) and five genera (*Mescalites, Juresanites, Prostacheoceras, Kargalites,* and *Tabanta-*

lites) at the beginning of the Asselian Stage, and one family (Eothititidae) with eight genera at the initial phase of the Artinskian Stage. Short periods of biota formation were followed by speciation and expansion outbreaks which more or less lasted until the deep final crisis.

It should be noted that the description of ammonoid evolution presented here is too generalized, because ammonoid finds and their complete successions in geological sections are too sporadic. The description is chiefly based on data from the Urals, where the transition from Sakmarian to Artinskian ammonoids is most evident, and traces of the Artinskian regression are insignificant (Ruzhentsev, 1951, 1952, 1956; Bogoslovskaya, 1962, 1988; Chuvashov and Bogoslovskaya, 1981). In other regions, which were more intensively affected by this regression, the difference between the Sakmarian and post-Sakmarian assemblages of ammonoids may contrast even more (Leven et al., 1992; Furnish and Glenister, 1977).

CONODONTS

The Early Permian history of conodonts is distinctly divisible into three intervals (Fig. 4), when their dominant forms were successively represented by streptognathoids, neogondolelloids, and neostreptognathoids (Barskov and Reimers, 1992). The first of them corresponded to the Asselian Stage, with abundant conodonts of the genus *Streptognathodus*. The next interval corresponding to the Sakmarian Stage is marked by the predominance of the *Neogondolella* species, whose first occurrence level is in the Asselian deposits. The maximum diversity of this genus is confined to the first half of the Sakmarian Stage, when it included at least nine species, all represented by larger forms. The crisis in their evolution was at the end of the stage, and only one species, *Neogondolella bisselli*, survived this event (Ritter, 1986).

The origin of new genera *Sweetognathus* and *Neostreptognathodus*, coeval with the decline phase of *Neogondolella*, symbolized the beginning of the third period in conodont evolution. In the Urals, the first primitive forms of the genus *Sweetognathus* appeared in the uppermost Sakmarian horizons. The first conodont specimens with deep axial sulculus, such as *Neostreptognathodus obliquidentatus*, *N. pequopensis*, and *N. exculptus*, were recorded at the base of the Artinskian strata (Chernykh, 1989). Here, they are associated with the widespread species *Sweetognathus withei*. In Tethyan regions, these species occur at the base of the Yakhtashian Stage, or immediately below it (Zhou Zuren, 1988; Zhang Linxin, 1988). According to the fusulinid scale, this lower level should be assigned to the Sakmarian Stage, however, according to conodonts, it is correlative with the lowermost Artinskian beds of the Urals, and this solution seems to be more correct. In North America, as in the Urals, the most primitive *Sweetognathus* forms occur somewhat lower

than *Sw. withei* and the first representatives of the genus *Neostreptognathodus*. The last forms were reported from the uppermost part of the Lenox Hills Formation bearing, as was already mentioned, the Sakmarian ammonoids.

Thus, the data above suggest that the foremost elements of the *Neostreptognathodus* assemblage signifying the new stage in conodont evolution appeared at the Sakmarian–Artinskian boundary, a little before the rejuvenation stage distinguishable in fusulinid and brachiopod communities. The initiated changes in conodont assemblages underwent intense progress during the late Artinskian–Kungurian time, and resulted in a high diversity of *Sweetognathus* and *Neostreptognathodus* species. New genera *Pseudosweetognathus, Rabeignathus, Vjalovognathus,* and *Homeoiranognathus* also appeared during this interval. Another outbreak of speciation was typical of *Neogondolella* forms at the very end of the Artinskian time and throughout the Kungurian Stage. The maximum taxonomic diversity of conodonts is confined to the Kungurian (Bolorian) Stage. At the end of this interval, representatives of the *Sweetognathus* and *Neostreptognathodus* genera were under decline, whereas *Neogondolella* forms continued their evolution to become basic elements of the Late Permian conodont communities.

CONCLUSION

Our analysis of the Early Permian evolution of four main groups of marine fauna suggests the following conclusions:

(1) Despite different habitat environments, all the groups underwent an evolutionary crisis during the mid-Early Permian time, which was followed by a rejuvenation stage, when new elements typical of the Late Permian appeared in all communities.

(2) The crisis was confined to the Sakmarian–Artinskian boundary interval. The first results of rejuvenation are notable in the initial–middle interval of the Artinskian Stage, while the speciation outbreak was at the end of this stage and during the Kungurian (Bolorian) time. Having a great deal in common, the Asselian and Sakmarian assemblages show many features inherited from their Carboniferous ancestors. The Late Permian elements in rejuvenated assemblages of different groups were of dissimilar evolutionary significance.

(3) Other groups of fauna also experienced comparable changes during the stratigraphic interval under consideration (Astaf'eva and Astaf'eva-Urbaitis, 1988; Guseva and Koshevarova, 1984). These changes were most evident in the Boreal and Notal provinces, where transformations affected the biota altogether. For instance, during the Asselian–Sakmarian time, the Sverdrup basin of the Canadian Arctic was inhabited by tropical organisms (chlorosponge and chloroforam) with dominant groups represented by algae, foraminifers (fusulinids including), calcareous sponges, colo-

nial corals, and paleoaplisines. During the Artinskian and Kungurian stages, they were replaced first by moderately thermophilic (brionoderm-extended), and then by cryophilic (brionoderm) assemblages, the latter consisting of bryozoan, brachiopods, crinoids, and bivalves (Beauchamp, 1993). The same changes were also typical of the Timan–Pechora basin. Equal in significance, opposite evolutionary patterns were recorded in the peri-Gondwana regions of the Tethys, where the cryophilic Asselian community of the eurydesmo-conulariid type with associated bryozoan and brachiopods was replaced by the thermophilic assemblages of the late Yakhtashian–Bolorian time, which consisted mostly of fusulinids, corals, brachiopods, and different algae, the latter also represented by reef-building taxa.

(4) The crisis coincided with the initial moment of a global regression, which was at its maximum during the middle Artinskian interval. The late Artinskian rejuvenation of biota seems fit Boucot's principle (Boucot, 1975), which suggests that rates of new taxa generation are increasing when their habitat areas are decreasing during regressive cycles. However, the late Artinskian–Kungurian radiation of rejuvenated assemblages definitely corresponds to the transgression cycle.

(5) In addition to the direct transgressive–regressive influence, the biota evolution was evidently under the control of related paleogeographic changes that ceased, or opened connections between basins, thus transforming the migratory ways of fauna. The examples are the late Artinskian–Kungurian migration of some bivalve taxa from the Notal into the Boreal basins (Astaf'eva and Astaf'eva-Urbaitis, 1988), and the coeval expansion of boreal brachiopods into the northern Tethys (Grunt and Dmitriev, 1973).

(6) Climatic changes were also significant factors affecting the biota evolution during the stratigraphic interval under consideration. Their influence was most evident in basins located within high latitudes, where climatic fluctuations were the most contrasting.

(7) The late Sakmarian–early Artinskian biotic crisis and subsequent rejuvenation of biota are the results of many factors, and we do not know so far which one was the main and most influential among them. Nevertheless, it is clear that the Artinskian Stage corresponds to the critical moment of the Permian geological history, implying that the biotic and abiotic events of this stage should be evaluated to a greater extent than they have been.

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