

THE DYNAMICS AND BIOCHRONOLOGICAL STRUCTURE OF THE HANGENBERGIAN BIOEVENT

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ABSTRACT

The Hangenbergian (Devonian-Carboniferous) crisis in the evolution of paleobiota is analyzed by the reconstruction of some of the best known fossil groups with the involvement of data on their bed-by-bed distribution in the continuous sections of D/C boundary deposits. For this analysis the system-grounded biochronological approach is used, which provides a possibility for comparing the alterations in the composition and structure of zonal assemblages among different fossil groups in universal terms of persistent, tempoendemic (Devonian and Carboniferous), tempotonic (transitional) and ephemeridic archetypes.

INTRODUCTION

The Hangenbergian (Devonian-Carboniferous) crisis in the evolution of paleobiota is distinguished by two characteristics. First, by the drastic changes in the composition of paleobiota manifested by a sudden disappearance of Clymeniida, some groups of Trilobita (Phacopida), and Conodonta (Palmatolepis and Icriodus). These changes were concurrent with a new sedimentation pattern which is evident from the depressional zones of some European paleobasins (Walliser, 1984).

Secondly, the Hangenbergian event is established by the statistical calculation of the number of taxa of any rank which disappeared at or, more correctly, near the Devonian-Carboniferous limit (Raup and Sepkoski, 1984, 1986; Xu et al., 1989). The extinction rate of fossil families attained 20% and was caused by the disappearance of Clymeniida among ammonoidea, Discosordia among nautiloidea, Phacopida among trilobita, and all Placoderma. The same event may have caused the disappearance of Cyrtospiriferidea among brachiopods, Quasiendothyridae among foraminifera, some ostracoda and conodonta genera (mentioned above), and some other fossil groups. Still, it is noteworthy, that the idea that the Devonian/Carboniferous (D/C) event-caused extinction of all Discosordia and Placoderma is based on solitary findings of the last forms of these taxa in Upper Famennian deposits and does not involve the analysis of data on their bed-by-bed distribution for continuous sections of the D/C transition. Therefore, just the statistical information alone on the D/C (and, it seems any other) bioevent cannot provide a proper understanding of the disappearance of older Devonian organisms and the origination of new Carboniferous ones.

For this reason, I will first concentrate on the reconstruction of some of the best known fossil groups with the involvement of data on their *bed-by-bed distribution in the continuous sections* of D/C boundary deposits. Secondly, I will use for this analysis the *system-grounded biochronological approach*, which provides a possibility for comparing the alterations in the composition and structure of zonal assemblages among different fossil groups in universal terms of persistent, tempoendemic (Devonian and Carboniferous), tempotonic (transitional) and ephemeridic archetypes (Simakov, 1993).

THE DYNAMICS OF THE HANGENBERGIAN BIOEVENT

Ammonoidea. The D/C limit is signified by the first crisis in Ammonoidea evolution which nearly resulted in its full extinction (Bogoslavsky, 1988). A revision seems necessary of the idea that there was a sudden disappearance of *all* Clymeniida which was due to drastic environmental changes. This revision should also involve data of the ammonoids distribution in depressional sections. Indeed, clymeniids continued their existence after the deposition of cephalopod-bearing limestone ceased, even in some sequences of the Ruhr basin such as Drewer (Korn, 1988). And the last representatives of Clymeniida were discovered in *Acutimitoceras*-bearing strata of Mussenberg section (Korn, 1989).

In the case of rigorously simultaneous bedding in deposits of Hangenberg and Changshun shales in the Ruhr and Guizhou basins, clymeniids successfully survived the drastic environmental changes caused by the cessation of carbonate sediment deposition and wide distribution of "Hangenberg" shales in some of Guizhou sections such as Nanbiancun (Yu, 1988).

Therefore, an assumption is possible that the extinction of Clymeniida was not catastrophic in character, but proceeded gradually or stepwise, though it was quicker than the disappearance of Devonian taxa in other fossil groups (Fig. 1).

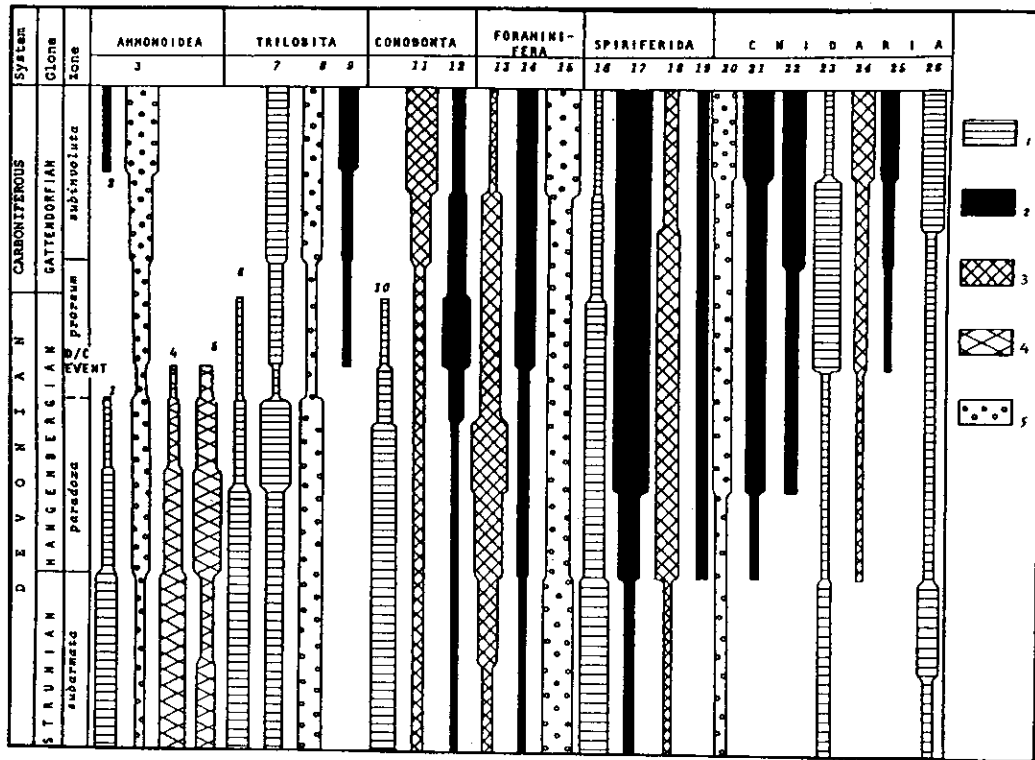


Fig. 1. Distribution of some fossil groups in the D/C boundary sequences.

Taxa archetypes: 1 - Devonian, 2 - Carboniferous, 3 - transitive, 4 - ephemerid, 5 - persistent. 1 - *Tornoceratina*, 2 - *Prolecaetina*, 3 - *Prionoceratidae*, 4 - *Clymeniina*, 5 - *Gonioclymeniina*, 6 - *Phacopidae*, 7 - *Proetidae*, 8 - *Archegoninae*, 9 - *Weaninae* + *Cystospirinae*, 10 - *Palmatolepis*, 11 - *Siphonodella*, 12 - *Protognathodus*, 13 - *Quasiendothyridae*, 14 - *Endothyridae* + *Chernyshellinae*, 15 - *Parathuramminidea*, 16 - *Cyrtospiriferidae*, 17 - *Spiriferidae*, 18 - *Sphenospira* + "*Hunanospiriferinae*", 19 - *Syringothyridae* + *Choristitidae*, 20 - *Syringoporidae*, 21 - *Thecostagitidae*, 22 - *Favositidae*, 23 - *Tabulophyllum*, 24 - *Tabulophylloidea* (sensu Onoprienko, 1979), 25 - *Caninidae*, 26 - *Stromatoporoidea*.

Trilobita. The D/C limit is significant by the extinction of Devonian *Phacopidae* and cardinal compositional changes among *Proetidae* and *Phillipsiidae*. The majority of Devonian trilobites did not survive these drastic environmental changes through the *Middle praesulcata* in basinal sequences evidencing a sharp replacement of cephalopod-bearing limestones by "Hangenbergian" shales. This permits us to connect the disappearance of Devonian trilobites with the Hangenbergian lithoevent (Walliser, 1984).

Still, from the *Upper praesulcata* are evident rare Devonian *Phacopidae* (*Omegops*) in South China (Ji et al., 1989) and the last Devonian *Proetidae* ("*Drewermannia*") in Ruhr basin (Alberti et al., 1974). The last *Phacops* occur at the bottom of the *sulcata*-zone in the La Serre section, which is the D/C boundary stratotype (Flais and Feist, 1988).

Thus, the extinction of Devonian trilobites proceeded in a peculiar "catastrophic-gradual" stepwise way. It should be emphasized, that the first Carboniferous *Phillipsiidae* (*Belgibole* and *Phillibole*) are evident from the *Upper praesulcata* in the Stockum and Grüne Schneid sections and co-occurs with the Devonian "*Drewermannia*" Moravica in the former (Alberti et al., 1974; Schönlaub et al., 1989).

Conodonts. The D/C event caused the disappearance of at least two Devonian conodont genera characteristic of deep- and shallow-water biofacies, that is *Palmatolepis* and *Icriodus*, respectively. According to the available data, the extinction of these genera was gradual due to a successive disappearance of the species. Such a successive disappearance is used to distinguish between the subzones of conodont zonation (Ziegler and Sandberg, 1984; Sandberg and Dreesen, 1984). However, this succession is different in various paleobasins (and even in the same one), so the extinction of the representatives of the same species was not simultaneous in different areas (Simakov, 1986).

The first conodonts characteristic of the Gattendorfian (that is *Protognathodus* and *Siphonodella*) began to occur during the Strunian. Their origination is not correlative with any events causing the disappearance of even

the separate representatives of the Devonian *Palmatolepis* and *Icriodus* genera. Neither the extinction of *Palmatolepis* and *Icriodus* nor the origination of *Protognathodus* and *Siphonodella* is correlative with the Hangenbergian lithoevent. Thus, the last *Pa. gracilis* are evident from above the "Hangenberg" black shales in the Nanbiancun section (Yu, 1988), and the first *Pr. meischneri* and *S. praesulcata* are known from the lower portion of *Wocklumeria-genozone* everywhere. Therefore, the processes causing the extinction of the older conodonts cannot be explained by a momentary universal factor.

Foraminifera. Until recently, the D/C boundary was considered to be best traced by the replacement of *Quasiendothyra*- by the so-called *Bisphaera-assemblage* in shelf (carbonate) facies. This drastic change is evident from the Dinant, Donetsk, Volga-Urals, and other paleobasins in West and East Europe. A more or less important sedimentation break is established between Devonian and Carboniferous deposits in all of these paleobasins. As a result, the deposits yielding *Bisphaera-assemblage* are underlain by beds bearing non-contemporaneous *Quasiendothyra-assemblage* in different paleobasins: this is *kobeitusana* in Dinant paleobasin, *konensis*- in the Donetsk, rare ("surviving") *Quasiendothyra* in South Urals, etc. On the whole, the disappearance of *Quasiendothyridae* was gradual, but not sudden. The last *Quasiendothyra* occur also in the deposits of Early Tournaisian in West Europe (Conil and Paproth, 1968; Kalvoda and Kukal, 1987).

Quasiendothyridae existed until the end of the Gattendorfian in some paleobasins of the Pacific realm (Simakov, et al., 1983). This may be explained by a relatively constant pattern of sedimentation there and, consequently, stable conditions for foraminifers at least through the Hangenbergian and Gattendorfian.

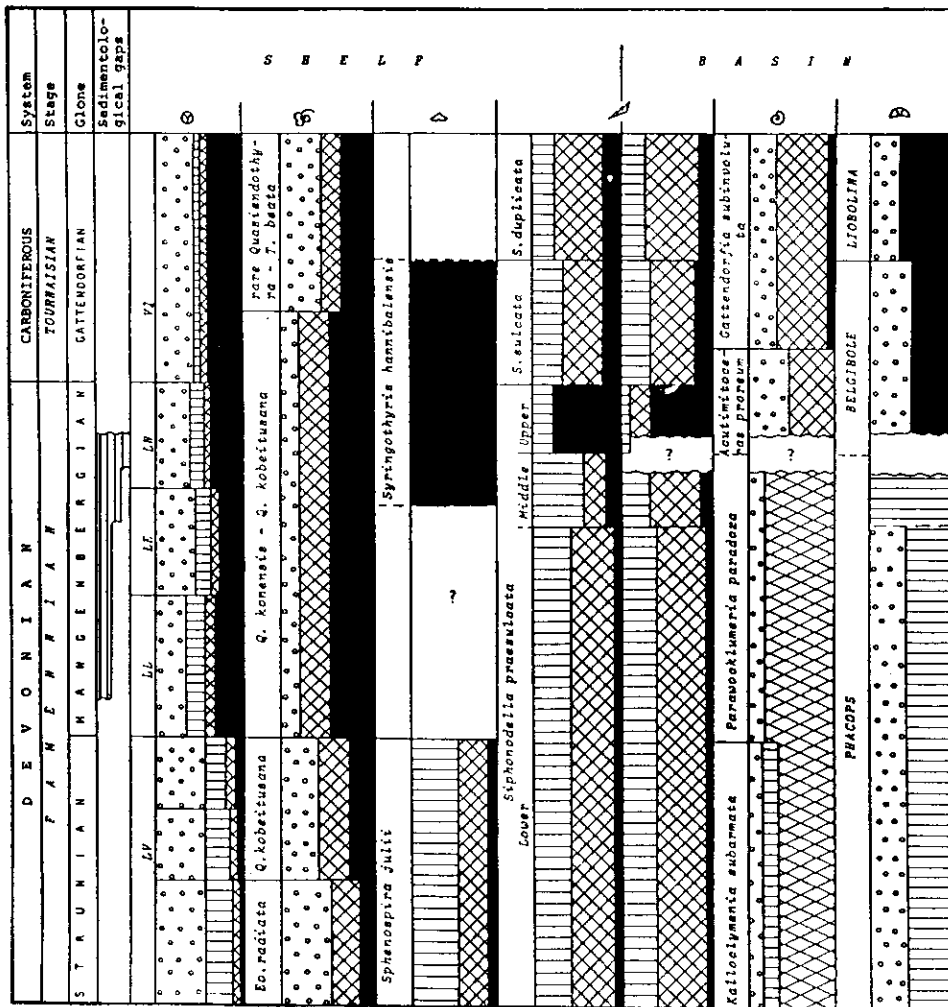


Fig. 2. The biochronologic structure of different fossil group zonal assemblages from the D/C boundary sequences in the West European basins (for symbols, see Fig. 4).

Thus, the disappearance of *Quasiendothyridae* cannot be explained as due to any universal factor which could be instantly disastrous for them throughout the Atlantic and Pacific realms. On the contrary, the *Quasiendothyra-assemblage* was replaced by the *Bisphaera-assemblage* at different times in different paleobasins and depended on changes in sedimentation patterns. *Quasiendothyridae* continued to exist under the favorable environment until the end of the Gattendorfian in some paleobasins.

The first representatives of the Carboniferous foraminifers (*Endothyridae* and *Chernyshellinidae*) began to occur during the Strunian, but they became dominant among foraminifers only in the

Middle Tournaisian. Thus, the origination of Carboniferous foraminifers and extinction of Devonian ones were parallel processes and cannot be explained as due to the same single reason.

Brachiopoda. A peculiar aspect of Famennian brachiopod-assemblages is determined by the wide-spread distribution of *Cyrtospiriferidae*, and that of Tournaisian assemblages is due to *Spiriferidae* and *Syringothyridae*.

Like foraminifers, the disappearance of Cyrtospiriferidae was influenced by environmental changes and was not simultaneous in different paleobasins. The last Molandispirifer existed in Kazakhstan, North-East of Russia, and other areas until the end of the Gattendorfian (Simakov, 1990).

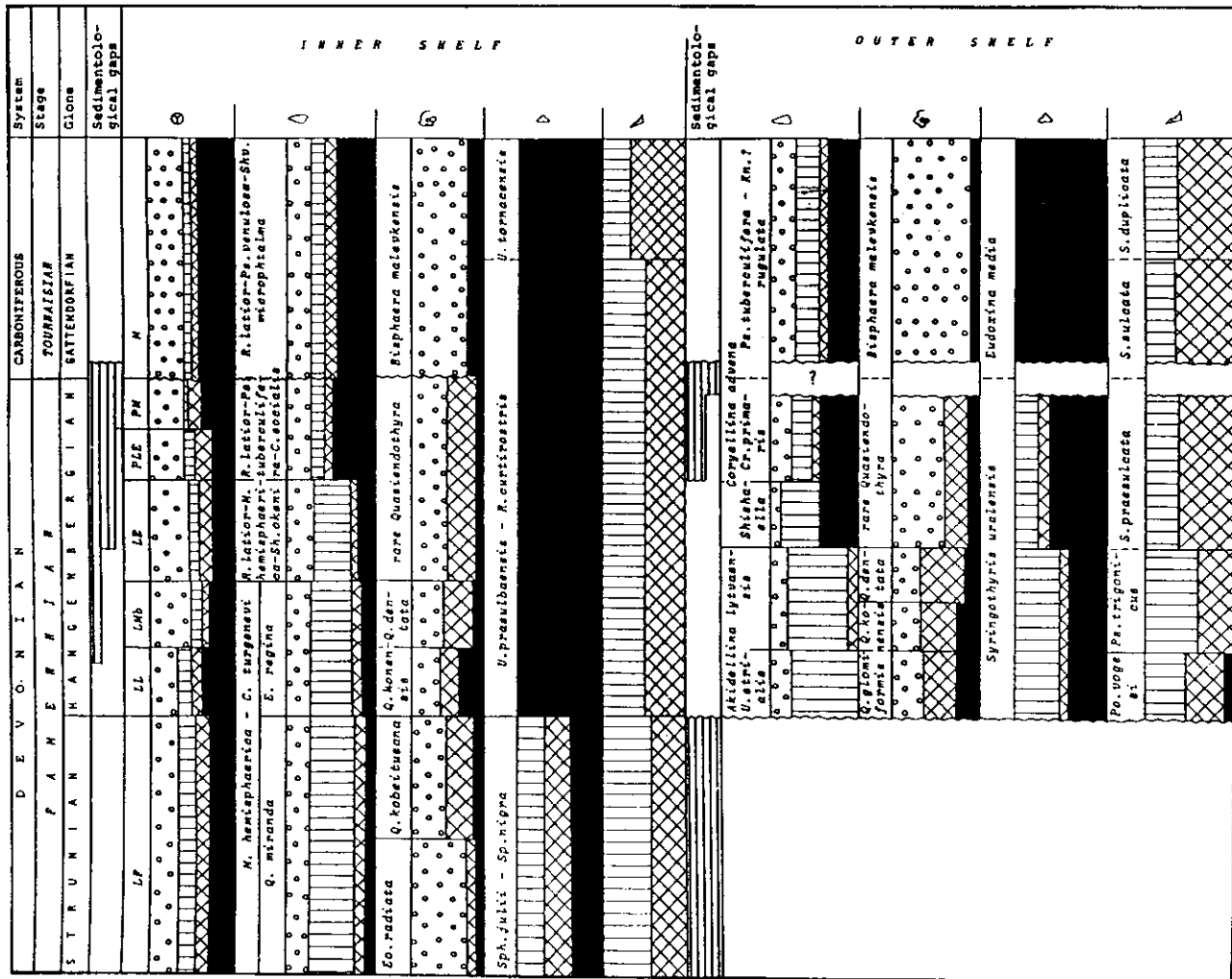


Fig. 3. The biochronologic structure of different fossil group zonal assemblages from the D/C boundary sequences in the East European basins (for symbols, see Fig. 4).

The first Spiriferidae (Unispirifer) began to occur during the Strunian (Conil et al., 1986). But the majority of Carboniferous Spiriferidae and Syringothyridae appear in the early Hangenbergian and were approximately concurrent with the last morphogenesis outburst among Clymeniida (House, 1985; Simakov, 1990). An assumption is possible that this was not accidental, but due to a universal factor influencing the morphogenesis of the living organisms inhabiting both the deep- and shallow-water conditions. I would like to stress, that this bioevent preceded the Hangenbergian lithoevent.

Corals. The overwhelming majority of Devonian reef-building coelenterates were obliterated during the Fr/Fa crisis. The first Carboniferous tetracorals began to occur during the Strunian (Poty, 1986). But, it was through the Hangenbergian and Gattendorfian that the morphogenesis of typical Carboniferous Cyathopsidae and Uraliniidae continued (Onoprienko, 1979).

The most ancient Carboniferous Thecostegitidae (Fu-chungopora) began to occur at the beginning of the Hangenbergian. The Carboniferous Favositidae originated in the middle Hangenbergian (Michelinia and Roemeripora) and earliest Gattendorfian (Yavorskya) (Smirnova, 1979).

The beginning of the Tabulophyllum morphostructural diversification, which resulted in Cyathopsidae and Uraliniidae archetypes (Onoprienko, 1979), and the origination of the Carboniferous Thecostegitidae took place in the early Hangenbergian. It is noteworthy, because these processes were approximately coincident in time with

the appearance of Carboniferous Spiriferidae and new major taxa Parawocklu-meriacea and Wocklumeriidae among Clymeniida. The initiation and stabilization of Carboniferous archetypes, both among tetracorals and tabulate corals, continued through the Hangenbergian and Gattendorffian and proceeded differently in various phyletic lineages (Onoprienko, 1979; Smirnova, 1979).

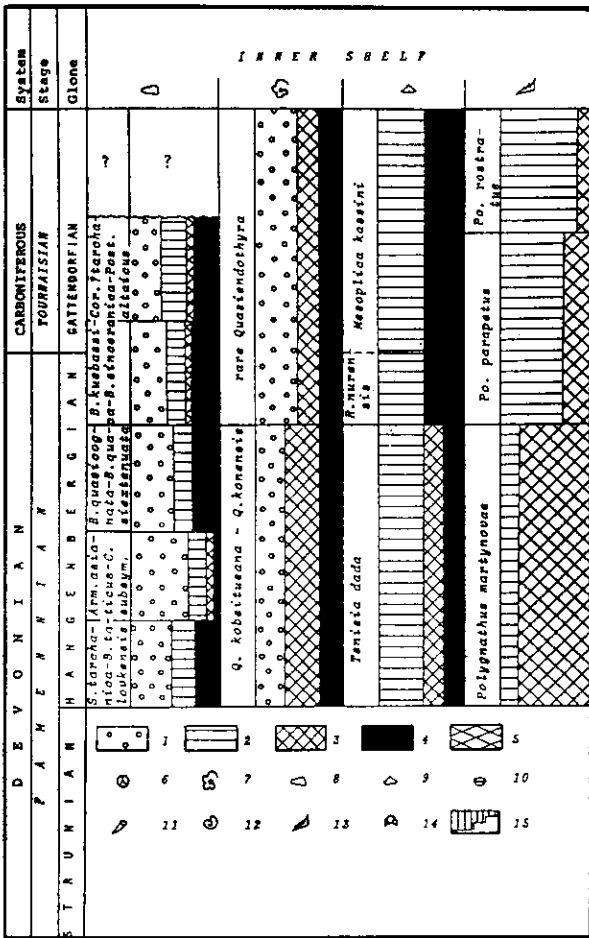


Fig. 4. The biochronologic structure of different fossil group zonal assemblages from the D/C boundary sequences in the Kazakhstan-Altay basins.

Taxa archetypes: 1 - persistent, 2 - Devonian, 3 - transitive, 4 - Carboniferous, 5 - ephemerid; *fossil groups*: 6 - spores, 7 - foraminiferes, 8 - ostracodes, 9 - brachiopods, 10 - tabulates, 11 - rugoses, 12 - ammonoids, 13 - trilobites, 14 - conodonts; 15 - sedimentation breaks in some paleobasins.

Stromatoporoids. Until recently, stromatoporoids were considered to disappear at the end of the Famennian (Conil, 1961). But according to new evidence (Simakov et al., 1983), they co-existed with Quasiendothyridae and the last Cyrtospiriferidae in the Omolon paleobasin until the end of the Gattendorffian. It seems a valid assumption that Stromatoporoidea disappeared just at the end of Gattendorffian in other paleobasins of the Pacific realm as well (Tong et al., 1985). In any case, there are no grounds to relate the overall disappearance of stromatoporoids to the D/C event.

Thus, the concurrent-range distribution that exists within the *Upper praesulcata* for Devonian and Carboniferous taxa of trilobites, foraminiferes, brachiopods, and other fossil groups is established.

I'd like to stress the following without dwelling on the processes of extinction of Devonian taxa and origination of Carboniferous ones in other fossil groups. The available data do not corroborate the hypothesis holding a sudden, momentary extinction ("mass killings" - McLaren, 1988) of different groups of Devonian fauna. This process was not simultaneous and occurred at different rates in various faunal groups. Extinction was gradual through the Strunian and

Hangenbergian and terminated by the end of the latter timespan in the *Palmatolepis* and *Icriodus*. It was much faster and occurred through the second half of the Hangenbergian among Clymeniida and Phacopida. In the end, the rate and duration of extinction processes were directly dependent upon the pattern of environmental changes, so that some groups such as Quasiendothyridae, Cyrtospiriferidae, and Stromatoporoidea, continued their existence in some areas until the end of the Gattendorffian.

There are no facts confirming the supposition that the first occurrence of new Carboniferous taxa in any group is separated from the disappearance of older Devonian ones by a "free" space-time interval yielding just the persistent forms. Such an evolutionary pattern is valid only for Ammonoids with a very short late *Acutimitoceras* space-time interval between the last Clymeniida and first Prolecanitina and Gattendorfia stratigraphic ranges. The first representatives of Carboniferous taxa began to occur in other fossil groups during the Strunian, with their mass distribution since the early Hangenbergian through Gattendorffian, side by side with disappearing Devonian taxa. In other words, Carboniferous forms occupied the ecological niches not because they became suddenly vacant, but rather due to a gradual displacement of Devonian ones. It is noteworthy, that the beginning of the morphostructure diversification among tabulates and tetracorals, which resulted in the Carboniferous archetypes, and also the mass occurrence of the latter among spiriferids, were concurrent with the last outburst in morphogenesis among clymeniids, which marked the beginning of the Hangenbergian. Maybe, the coincidence of these essentially different bioevents was not fortuitous, but it does not seem possible to explain it from the viewpoint of any universal outer factor which could influence such biologically diverse organisms.

Fourthly, the first taxa with "transitive" and Carboniferous archetypes began to occur already during the Strunian in all groups except Ammonoidea and Trilobita. But the majority of them originated through the Hangenbergian. It is interesting that, despite the irregular character of this process in space and time, taxa with new archetypes began to occur much earlier among inhabitants of the shallow water, whereas they appeared among inhabitants of the deep water through the late Hangenbergian - early Gattendorfian.

Thus, the examination of the structure of the D/C biota transition proves that this process was gradual or step-wise and metachronous among various fossil groups and irregular in space and time. The appearance of liberated ecological niches in all environments, and the origination and subsequent distribution of taxa with Carboniferous archetypes cannot be considered as resulting from a momentary event due to a sudden effect of any universal factor which influenced the entire paleobiota in a shock-like manner causing the mass extinction of taxa with Devonian archetypes in all faunal groups.

CONCLUSIONS

According to the analytical treatment of the bed-by-bed distribution of Devonian and Carboniferous taxa in the continuous D/C boundary sequences, the extinction of the first ones and origination of the last ones proceeded simultaneously and in metachronous way in different fossil groups with no representatives of the same group undergoing these changes. One may paraphrase the well-known words of Mark Twain, that the rumors of the demise of biota by drastic and dramatic mass extinction during the Hangenbergian event have been greatly exaggerated.

I would like to stress here, that the extinction of Devonian taxa representatives proceeded due to their gradual or step-wise elimination or their sudden disappearance in different groups and even within the same group but in different paleobasins. These processes occurred through different time-spans, the duration of which was dependent on the pattern and rate of the environmental changes for the different groups and paleobasins. It is noteworthy, that the drastic changes in the sedimentation pattern were not coincident with but were preceded by the disappearance of Devonian taxa in all paleobasins. In other words, the disappearance of Devonian taxa resulted from the ecosystem alteration in any paleobasin. Consequently, *the use of the extinction event records to mark and globally trace chronostratigraphic boundaries can't essentially provide their isochronous character.*

In my opinion, the origination of Carboniferous taxa with essentially new archetypes in some fossil groups, which successfully replaced Devonian ones, was the most important result of the D/C bioevent. Carboniferous taxa began to appear during the Strunian and the process continued in a metachronous way in different groups through the Hangenbergian and Gattendorfian. It is essentially important, that the origination of taxa with new archetypes is not in anyway correlative with any outer factors resulting in mass extinction of Devonian faunas and drastic environmental changes. This circumstance again leads us to consider the hypothesis, which could explain the evolutionary and morphostructural alterations finding their expressions in the appearance of taxa with new archetypes, as due to the autonomous laws of biologic evolution but not any outer factors (cf. Schindewolf, 1950). I think, the data presented in this paper and the other information available regarding the origination of taxa with new archetypes is not the least contradictory to this conception. And this much argues in favor of using the records of origination of taxa with new archetypes but not the extinction of the older ones to establish and trace the chronological boundaries.

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