Veröffentlichung des Österreichischen Nationalkomitees für das International Geological Correlation Programme (Project Nr. 4 Triassic of the Tethys Realm. Project Nr. 106 Permo-Triassic Stage of Geological Evolution)

Palaeosuccessions and the Basic Factors of Syngenesis During the Time of the Permian-Triassic Boundary

By YURI D. ZAKHAROV*

With 5 figures and 3 tables

(Vorgelegt in der Sitzung der mathem.-naturw. Klasse am 24. Juni 1983 durch das w. M. H. ZAPFE)

Introduction

Studies on peculiarities of biota change at the turn of different epochs of the geological past are of great importance to comprehend general regularities of macroevolution. The palaeoecological data are of particular interest in connection with this problem. One of the largest Phanerozoic boundaries, the Palaeozoic-Mesozoic one is palaeoecologically not well enough investigated. Recently J. VALENTINE (1969) noted rightly that there are too few data on the ecological hierarchy of the Permian-Triassic time. Original peculiarities at the end of the Permian left their imprint on nature of the Permian-Triassic boundary sediments (there are stratigraphical interruptions in the majority of well-known sections). The fullest sections of the Upper Permian marine sediments were recognized only within three regions: Trans-Caucasus, Iran and South China.

The present work is an attempt to analyse the Permian-Triassic palaeosuccession of Trans-Caucasus on the basis of material collected by Drs. G. V. KOTLJAR, B. V. KOCZYRKEVICZ, G. S. KROPATCHEVA, K. O. ROSTOVCEV, I. O. CHEDIJA, and G. P. VUKS (KOTLJAR, ZAKHAROV et al., in press) and data presented in the collective monograph of Palaeontological Institute, USSR Academy of Sciences (RUZHENCEV and SARYCHEVA, 1965).

Method of analysis

It is well known that even thin beds of sediments have been deposited usually during a long period of time, incomparable with a human life span. Therefore, the palaeosuccessions (KRASSILOV, 1970, 1977) in contrast to the successions distiguished on the basis of recent organisms, reflect only the greatest changes of community structure. In this connection a use of CLEMENTS' (1916, 1936) terms in palaeoecology seems to be not always appropriate. The palaeosuccession phases are essentially

*Dr. YU. D. ZAKHAROV, Institute of Biology and Pedology. Far-Eastern Sciences Centre, USSR Academy of Sciences. 690022, Vladivostok, USSR.

controlled by the time change of taxonomic diversity in various organism groups, composed of certain communities. The maximum of taxonomic diversity is known to be typical of communities which existed under the most favourable conditions. According to R. MARGALEF (1968) a great taxonomic variety means long trophic chains. The large number of species is characteristic of communities of tropical regions, thus being represented by a fewer number of individuals per unit of the area than species of temperate regions (degree of an equalization for distribution of individuals in tropical species is largely expressed).

The taxonomic diversity was calculated in the present work by two indices:

(1) index of the species abundance (d) and

(2) index of the degree of equalization for distribution of individuals between species (K), the last one is proposed to be estimated due to the maximum difference in frequency of species occurence.

$$(1)\ d = \frac{S-1}{\log N}$$

S = number of species
N = number of individuals (ODUM, 1975).

$$(2)\ K = F\max - F\min = \frac{n\max}{N} \cdot 100\ \frac{n\min}{N} \cdot 100$$

F max = occurence frequency of the dominant species.
F min = occurence frequency of the most scanty species.
n max = number of individuals of the dominant species.
n min = number of individuals of the most scanty species.
N = number of individuals of all the species.

The maximum values for species abundance (d) and the minimum values for index of the degree of equalization (K) are representative of the highest species variety.

Characteristics of the basic palaeosuccessions

1. Trans-Caucasus

In the Trans-Caucasus palaeosuccession during the late Midian (Permian)-early Induan (Triassic), five phases can be distinguished, reflecting a degree of diversity for the marine communities which existed at that time (Fig. 1). In composition of the Permian producers of Trans-Caucasus the red and green algae are known; the consumers were foraminifers, Sphinctozoa, corals, Bryozoa, brachiopods, gastropods, nautiloids, ammonoids, ostracodes, trilobites, conodont organisms and rarely fishes. Only a part of these groups kept existing in this basin during early Triassic time.

During phase 1 (end of Midian stage), a main body of the community was formed by foraminifers and brachiopods. This was the time for

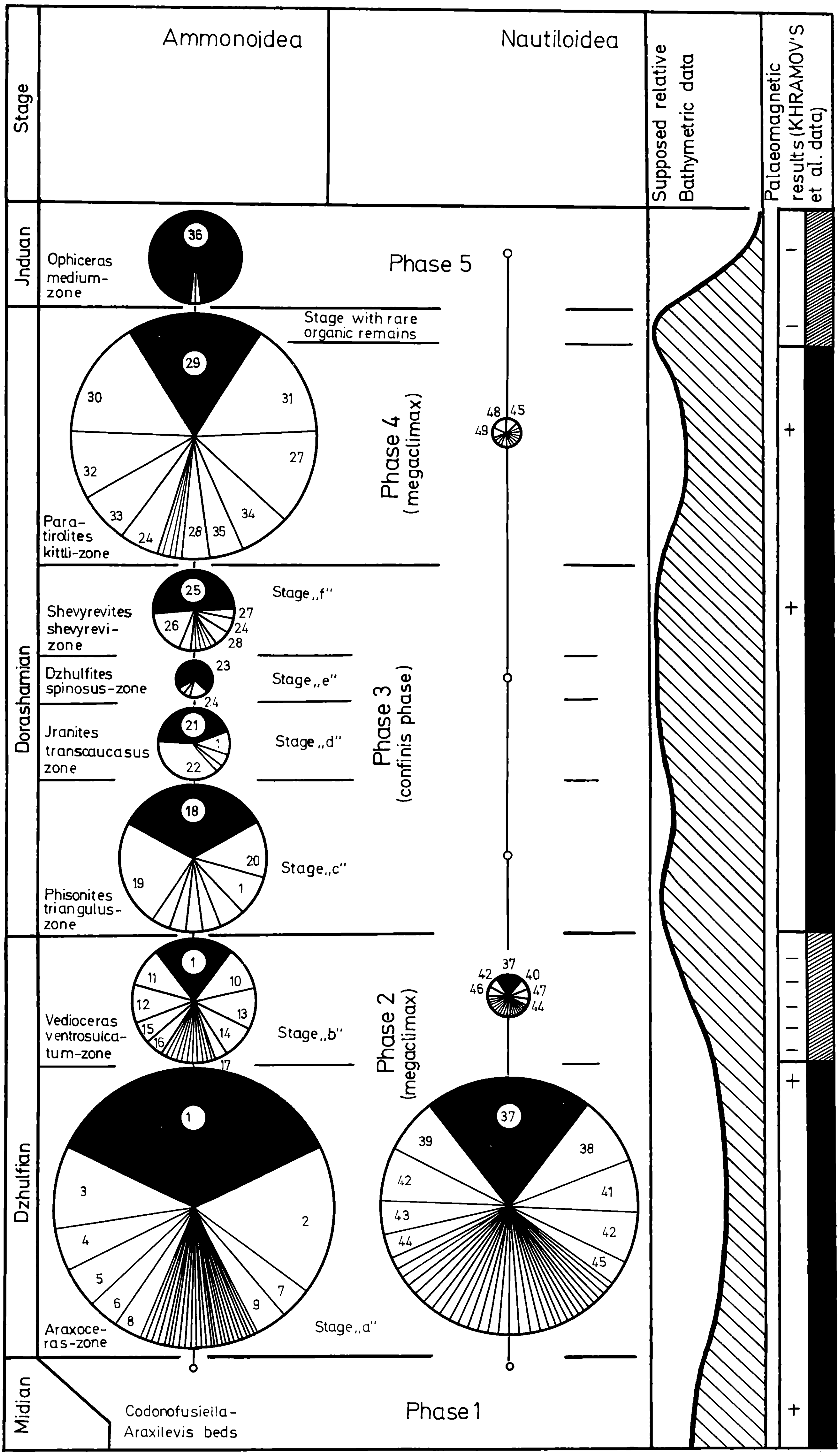

Fig. 1: Palaeosuccession of Permian-Triassic cephalopod faunas in Trans-Caucasus. Diameter of each ring is proportionate to the abundance of zone complexes; the species diversity is shown by the number of sectors; sector area is proportionate to the quantity of corresponding species; a dominant species is indicated by the black colour. 1 – *Pseudogastrioceras abichianum*, 2 – *Vescotoceras parallelum*, 3 – *V.* sp., 4 – *V. acutum*, 5 – *Prototoceras tropitum*, 6 – *Vescotoceras serratum*, 7 – *V. evanidum*, 8 – *V. pessoides*, 9 – *Araxoceras latum*, 10 – *Avushoceras jakowlewi*, 11 – *Vedioceras ogbinense*, 12 – *V umbonovarum*, 13 – *V* sp., 14 – *V. ventroplanum*, 15 – *V. ventrosulcatum*, 16 – *Dzhulfoceras fürnishi*, 17 – *Avushoceras* sp., 18 – *Xenodiscus araxensis*, 19 – *Phisonites triangulus*, 20 – *Xendicus dorashamensis*, 21 – *Iranites transcaucasius*, 22 – I. sp., 23 – *Dzhulfites spinosus*, 24 – *Dzhulfitidae* gen. et sp. indet., 25 – *Shevyrevites shevyrevi*, 26 – *Sh.* sp., 27 – *Abichites stoyanowi*, 28 – *Abichites* sp., 29 – *Paratirolites vediensis*, 30 – *Sinoceltites? minutus*, 31 – *Paratirolites* sp., 32 – *P. waageni*, 33 – *P. trapezoidalis*, 34 – *Abichites mojsisovicsi*, 35 – *Paratirolites kittli*, 36 – *Ophiceras (Lytophiceras) medium*, 37 – *Neocycloceras margaritatum*, 38 – *Pleuronautilus incertus*, 39 – *Neocycloceras obliqueannulatum*, 40 – *Domatoceras gracile*, 41 – *Alexandronautilus abichi*, 42 – *Lopiongoceras lopingense*, 43 – *Alexandronautilus* sp., 44 – *Pseudotitanoceras armeniacum*, 45 – *Cycloceras bicinctum*, 46 – *Pleuronautilus* sp., 47 – *Pseudotemnocheilus* sp., 48 – *Neocycloceras* sp., 49 – *Paranautilus* sp. Designation of the zones and beds: Cod. = *Codonofusiella-Araxilevis* beds, Ar = *Araxoceras latissimum* zone, Ved. = *Vedioceras ventrosulcatum* zone, Ph = *Phisonites triangulus* zone, Ir = *Iranites transcaucasius* zone, Dzh. = *Dzhulfites spinosus* zone, Sh. = *Shevyrevites shevyrevi* zone, Par. = *Paratirolites kittli* zone, Oph. = *Ophiceras medium* zone

invasion of the first ammonoids. The nautiloids were also infrequent at that time, but they appeared earlier than ammonoids in this basin (in the Arpian). Producers consist of red, as well as of green algae. Phase 2 (Dzhulfian stage) is characterized by an abundance and high taxonomic diversity of the most active consumers, cephalopods, which were represented by single individuals during the previous phase. Producers were mainly composed of the red algae (they had an extensive development apparently only in the beginning of Dzhulfian stage). The main body of community was formed by brachiopods.

During phase 3 (early Dorashamian, *Phisonites triangulus-Shevyrevites shevyrevi* zones), a sharp reduction in taxonomic diversity of all the groups inhabiting this basin, except ostracodes, had happened. The greatest changes took place in the structure of not mobile benthos (brachiopods, corals). The main body of the community was formed by ostracodes and ammonoids.

Phase 4 (late Dorashamian stage, *Paratirolites kittli* zone except its end) is characterized by the marked increase in abundance and taxonomic diversity of some invertebrate groups and, first of all, ammonoids. The main body of the community was formed by nautiloids and ammonoids.

The community structure was changed radically at the Permian-Triassic boundary. During phase 5 (early Induan stage, *Ophiceras medium* zone), foraminifers, corals, and brachiopods disappeared, the abundance and taxonomic diversity of cephalopods decreased sharply. Bivalves mainly of the genus *Claraia* became predominant in the community composition. Algae are newly widespread.

Fluctuation of the quantity

The quantity of various organism groups of Trans-Caucasus varied at the Permian-Triassic boundary (Fig. 2). The population peak of the foraminifers falls on phase 1. At the beginning of phase 2 of the Dzhulfian stage their abundance was sharply reduced (no less than 10–15 times), just increasing by the end of this phase. During the following phases of the Dorashamian stage, an abundance of foraminifers was even more reduced (they were not found at all within the *Iranites transcaucasius* and *Shevyrevites shevyrevi* zones). During phase 5 of the early Triassic they seemed to disappear. Maximum abundance of tetracorals is associated with the phase 4, and to a certain degree with 1 and 2. At the early Triassic they became extinct. Trans-Caucasus brachiopods were extensively widespread during the phase 1 and 2 (their population peak falls on the beginning of phase 2). During Dorashamian stage, brachiopod abundance was reduced by several hundred times. Within the Lower Triassic sediments of Trans-Caucasus no brachiopods have been found. Permian bivalves were observed in Trans-Caucasus only as single specimens; their abundance sharply increased during the phase 5 of early Triassic.

During phase 1, cephalopods were represented by rare individuals. Their population peaks fall on the beginning of the phases 2 and 4.

Ostracodes were the most numerous at the beginning of phase 3.

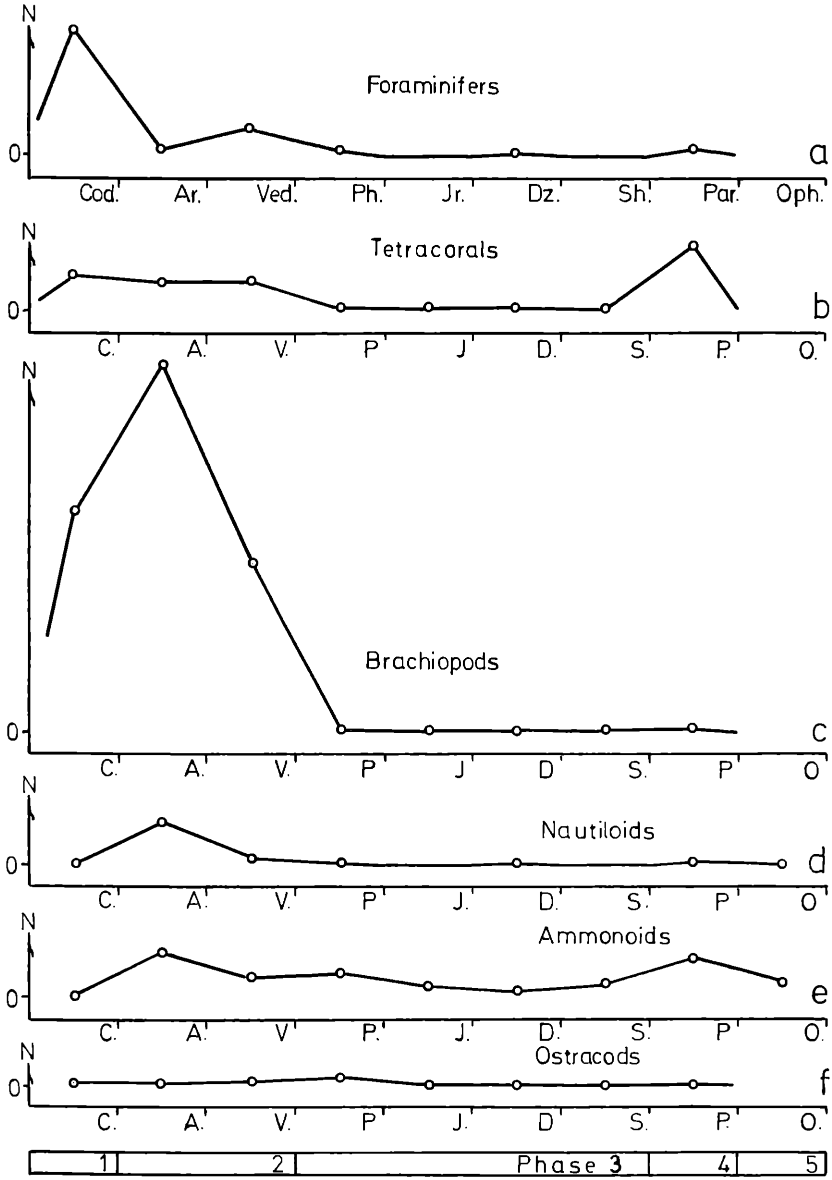

Fig. 2: Fluctuation of the quantity (N) of late Permian and early Triassic invertebrates of Trans-Caucasus. a – foraminifers, b – tetracorals, c – brachiopods, d – nautiloids, e – ammonoids, f – ostracodes. Designation of the zones as in Fig. 1.

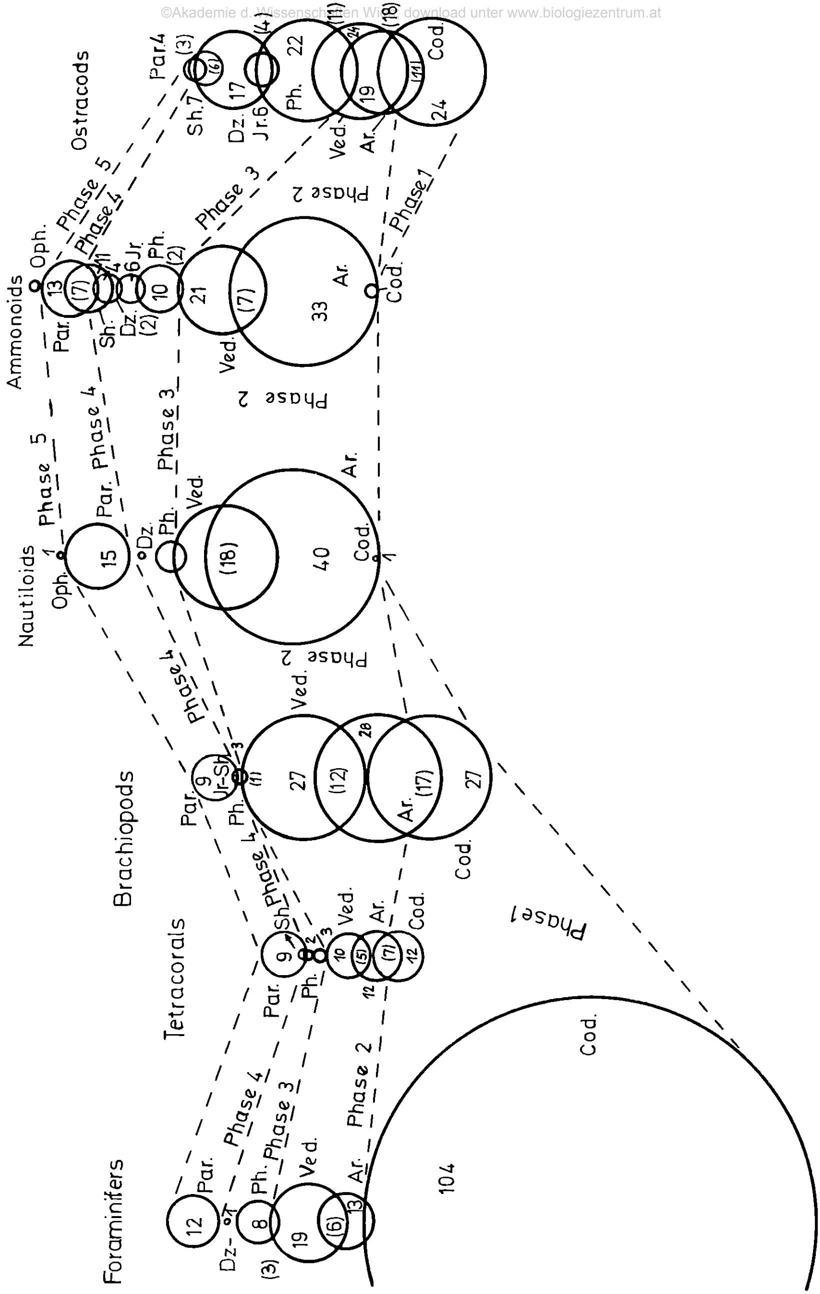

Fig. 3: Faunal succession during the Permian-Triassic in Trans-Caucasus. The zone complexes are shown in the form of a ring to the degree of change at the corresponding boundary; diameter of each ring is proportionate to the number of species; the figure in the ring is the number of species in the corresponding zone; the number of species in common with adjacent zones is shown in brackets. Designation of the zones as in Fig. 1.

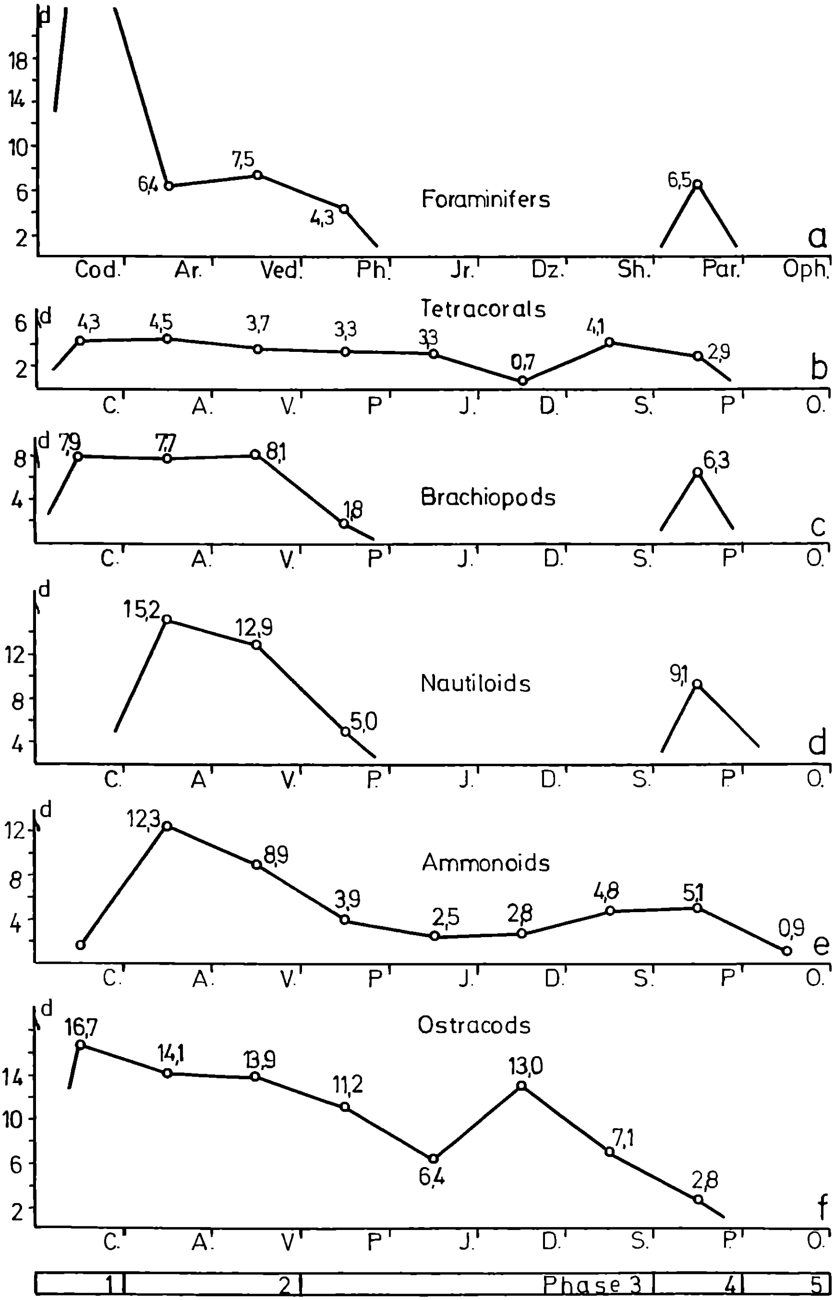

Fig. 4: Change of species abundance (d) of late Permian and early Triassic invertebrates in Trans-Caucasus. Designation of the zones as in Fig. 1.

Change of species abundance

The widest range of species of most groups studied, except foraminifers and ostracodes, is characteristic of the phases 2 and 4 (Fig. 3, 4). On the contrary, the maximum of foraminifere and ostracode species falls on phase 1.

Degree of equalization for distribution of individuals in the species

The maximum degree of equalization for individuals between foraminifere species falls on phase 1, brachiopod – phase 2, nautiloid and ammonoid – phase 2 and 4 (minimum values of the coefficient K). There are some problems in using this coefficient when the extracts are represented by rare specimens (Table 1).

Change of dominants

A change of dominance becomes apparent within every group of the palaeosuccession considered (Table 1). Within the phases 2 and 3 the palaeosuccession stages are distinguished on the basis of the marked modification of species composition and change of dominants. The stages a–b of the Dzhulfian are characterized by the change of brachiopod and foraminifer dominants, whereas the stages c–g of the Dorashamian are characterized by the change of nautiloid, ammonoid, and partially, brachiopod and tetracoral ones.

Faunal succession

The most considerable distinctions between phases and stages of palaeosuccession during the time of the Permian-Triassic boundary are established on the basis of ammonoid species composition (Table 2); a limited quantity of the early Dorashamian foraminifers, brachiopods and tetracorals makes it difficult to determine a degree of the faunal succession for these groups. Within the uppermost Permian zone of Trans-Caucasus (*Paratirolites kittli,* phase 4), small foraminifers, tetracorals, brachiopods, nautiloids, ammonoids, ostracodes, conodonts, and rare trilobites are known. Fish remains *(Helicampodus)* are likely to be found in these sediments. The uppermost beds of *Paratirolites kittli* zone, which lay under the Lower Triassic sediments, are comparatively poor in organic remains. In the Lower Triassic of Trans-Caucasus only algae, bivalves, gastropods, ammonoids, rare nautiloids and conodonts were found. Hence, the succession between faunas of phases 4 and 5 is the least expressed.

Change of lithofacies

During phase 1, sedimentation of various marine deposits took place in Trans-Caucasus (the section consists of dark grey and black limestones with chert lenses and nodules, black bituminous shales with aleurite dash). A sharp change of facies had happened within the greatest part of

Trans-Caucasus basin in phase 2 (Dzhulfian stage). The siliceous deposits are not observed in Dzhulfian strata. An increasing role of clay material and appearance of red colour clay-calcareous sediments are characteristic of the Dzhulfian stage (GULIEV et al., 1972). During the phases 3 and 4 (Dorashamian stage) the further changes of environments took place, which had an effect on peculiarities of sedimentation (increase of clay material and red colour sediments). In phase 5 (Induan stage) the sediments became less rich in clay material.

Palaeomagnetic results

According to new data by A. N. KHRAMOV and R. A. KOMISSAROVA based on the materials by KOTLJAR, ZAKHAROV et al. (in press), four palaeomagnetic zones can be distinguished within the Midian-Induan part of Trans-Caucasus succession:

(1) Late Midian–Early Dzhulfian zone of right polarity (*Codonofusiella – Araxilevis* beds and *Araxoceras latissimum* zone).

(2) Late Dzhulfian zone of reverse polarity (*Vedioceras ventrosulcatum* zone).

(3) Early Dorashamian zone of right polarity (observed only within *Shevyrevites shevyrevi* zone and lower part of *Paratirolites kittli* zone).

(4) Latest Dorashamian – Early Induan zone of reverse polarity (uppermost part of *Paratirolites kittli* zone and *Ophiceras medium* zone).

Palaeomagnetic results confirm the idea about marked inversion of the magnetic field during the Permian-Triassic boundary. According to palaeomagnetic data, KHRAMOV and KOMISSAROVA consider the Permian part of the Trans-Caucasus succession examined to be corresponding with the Upper Tatarian substage of the Russian Platform.

2. Central Iran

Conditions of sedimentation and peculiarities of development of marine faunas by the end of Permian and in the early Triassic of Central Iran are similar to those of Trans-Caucasus (BANDO, 1979; Iranian-Japanese Research Group, 1981). Here five phases of the palaeosuccession can also be distinguished, which seem to be synchronous with the adequate phases of Trans-Caucasus.

In the Midian (phase 1), the present area was occupied by foraminifers, brachiopods, rarely gastropods and bivalves; nautiloids and ammonoids were extremely rare (Table 3). Sediments of the Midian (Abadeh Formation) are represented by clay and siliceous-calcareous facies. This phase of palaeosuccession, like the one corresponding with Trans-Caucasus, may be characterized as the time for invasion of the first scanty ammonoids. The community composition abruptly changed in phase 2 of the Dzhulfian stage (the taxonomic diversity of cephalopods greatly increased, whereas the number of foraminifere and brachiopod species decreased). During the phase 2 the accumulation of clay-calcareous sediments took place. In the early Dorashamian (phase 3) a sharp reduction of taxonomic diversity of all the invertebrate groups, including cephalopods of Central Iran, has happened. By the end of the Dorashamian a taxonomic diversity of cephalopods noticeably increased. The accumulation of white and red calcareous facies was timed to the Dorashamian stage.

In the early Induan stage bivalves (*Claraia*) were mostly widespread. They formed the main body of community. The abundance and taxonomic diversity of ammonoids sharply decreased. Foraminifers, brachiopods, corals, nautiloids, and some other invertebrate groups known within the Permian sediments, have not been found in the Lower Triassic sediments. These sediments of Central Iran are represented by clay-calcareous facies.

3. South China

Various groups of the Permian-Triassic invertebrates of China have been studied to a different degree, which prevents the ecostratigraphical research. The most comprehensive information on ammonoids was obtained (ZHAO et al., 1978). Data on brachiopods, given in some publications, on the other hand have to be considerably verified and supplemented.

In the middle Midian stage the South China sea basin turned into a swampy plain, where an accumulation of coal sediments occured. Apparently, only by the end of this stage (phase 1) the marine conditions were re-established here with the result of the invasion of new settlers (foraminifers, brachiopods and rare cephalopods – Araxoceratidae?). During the Dzhulfian stage (phase 2) some parts of South China seas were occupied by a rather diverse fauna of cephalopods and brachiopods. During phase 2, in contrast to Trans-Caucasus, this region was characterized by the marked development of bivalves. Dzhulfian ammonoids of China were also more diverse than these of Trans-Caucasus. By the end of Dzhulfian stage, a sharp reduction in taxonomic diversity of all the invertebrate groups took place. In Changxing Province sandy-clay sediments (Laoshan shales) were accumulated during Dzhulfian time, whereas calcareous, rarely clay and siliceous-calcareous sediments (Wujiaping limestones, upper part) were distributed in Sychuan. Further decrease in the quantity and diversity of all the organism groups, except of foraminifers, is characteristic of the early Dorashamian time (phase 3). In Changxing Province, siliceous-calcareous sediments (Changxsing formation, lower part, disconformly overlapped the "Loping Series") were deposited at that time. In Sychuan Province the early Dorashamian sedimentation apparently has not taken place. During the late Dorashamian time (phase 4), the South China seas teemed with cephalopods, bivalves and also corals. Late Dorashamian ammonoids and brachiopods are more diverse than Trans-Caucasian. The Chinese fauna is also characterized by the development of bivalves. In Changxing Province calcareous sediments (Changxing limestones) were mostly accumulated;

while in Sychuan calcareous-clay and siliceous sediments (Dalong shales) were prevailing. The uppermost Permian beds in China are distinguished by the impoverished remains of the fauna.

The main body of the early Induan consisted of the bivalve fauna; ammonoids and brachiopods were less numerous than bivalves. Sediments are represented by clay-calcareous facies (thin-bedded grey limestones, dark-red shales).

Discussion

The clearly defined geocratical regime of the late Permian greatly influenced the peculiarities of the geographical differentiation of marine organisms. A high degree of the ammonoid endemism in Mediterranean and China regions (both on the generic and family levels) testifies the impeded connections between the late Permian seas even within the Tethys. A great variety of the east Tethys fauna is worth of notice.

The cited data also showed that marine communities were invariable during the Permian-Triassic. Within the palaeosuccessions examined, some consecutive phases can be distinguished.

The phases, in the course of which many or basic community elements acquire a high diversity, are proposed to be named as Megaclimax (descended from CLEMENTS' term Climax), whereas phases dividing Megaclimaxes as Confinis (from Latin word confinis = adjacent). The Confinis phases corresponding to the invasions of the first settlers can be designated as Pioneer ones.

In palaeosuccessions of the Tethys (Trans-Caucasus, Iran, South China) during the time of the Permian-Triassic boundary, some phases can be distinguished (Late Midian, Dzhulfian, Early Dorashamian, Late Dorashamian, and Early Induan) including two Megaclimaxes that evidently result from the global factors of the environment. The early Megaclimax phase falls on the Dzhulfian, the latter on *Paratirolites kittli* zone (except its end) of the Dorashamian.

There are contradictory views on the character of the climatic change by the end of the Permian and in early Triassic. Perhaps the mammal-like reptiles widespread in the late Permian were adapted to the warm and damp climate (DOTT, BATTEM, 1976). V. G. OCHEV (1960) polemizes with those investigators who prove an existence of desert conditions during the early Triassic. At the same time he considers that as a result of regression (OCHEV, 1973), a change of tetrapodes at the Permian-Triassic boundary could proceed under the general influence of a modifiable physiogeographic environment on the extended continents. In OCHEV's (1980) opinion, there are no reasons to disclaim also an effect of some cosmic factors on the Permian-Triassic faunas. V. A. VAKHRAMEEV, I. A. DOBRUSKINA et al. (1970) and S. V. MEIEN (1971) consider a wide development of coniferous and some xerophilous pteridosperms within Permian floras of the tropical zone to be an indicator for the increase of arid zones by the end of the Palaeozoic. In J. WATERHOUSE s' opinion, the highest Permian temperatures fall on the latest Dorashamian; M. I. BUDYKO (1981), on the contrary, considers the most outstanding fall of temperature during the Phanerozoic to be timed with the Permian-Triassic boundary.

To judge from the taxonomic diversity of ammonoids, the Roadian appeared to be the warmest stage of the Permian; during the following Permian stages, the temperature of sea waters on the whole apparently decreased (Fig. 5).

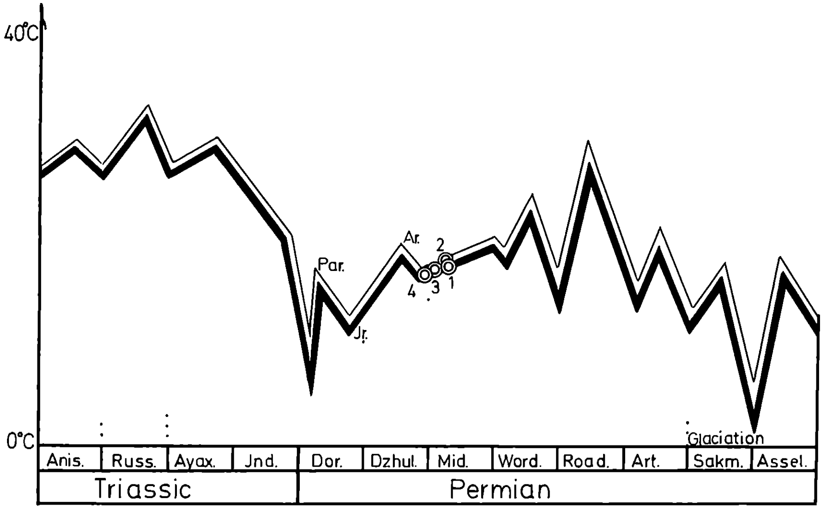

Fig. 5: Hypothetical world temperature changes based on taxonomic diversity of the Permian-Triassic ammonoids and isotopic composition of the Permian brachiopod shells (from Trans-Caucasus). 1 – $\delta\,^{18}O = -6.3$ ‰, $\delta\,^{13}C = +\,1.0$ ‰, "T"C = 48.7°; 2 – $\delta\,^{18}O = -6.8$ ‰, $\delta\,^{13}C = +\,2.1$ ‰, "T"C = 51.8°; 3 – $\delta\,^{18}O = -5.5$ ‰, $\delta\,^{13}C = +\,1.3$ ‰, "T"C = 44.1°; 4 – $\delta\,^{18}O = -4.2$ ‰, $\delta\,^{13}C = +\,2.5$ ‰, "T"C = 36.9°. Designation of the stages: Assel. = Asselian, Sakm. = Sakmarian, Art. = Artinskian, Road. =Roadian, Word. = Wordian, Mid. = Midian, Dzhul. = Dzhulfian, Dorash. = Dorashamian, Ind. = Induan, Ayax. = Ayaxian, Russ. = Russian, Anis. = Anisian. Designation of the zones as in Fig. 1.

The Paleozoic-Mesozoic boundary was the time for a great extinction in many groups of marine and terrestrial organisms. A considerable change of biota of that time may be related to a climatic peculiarity, an enormous eustatic fluctuation of the sea level, a strongest inversion of the magnetic field and other factors provoked by a change in the rotational regime of the Earth. The red colour rocks in the Upper Dzhulfian and the increase of their role in Dorashamian stage, may be due to a gradual increase of the seasonal prevalence of the late Permian climate. The early Induan invasion of cephalopod faunas of high-latitude regions in both hemispheres can be explained only by a visible rise of temperature of the subpolar waters. The increase of warmth in the beginning of Triassic time is likely to have been provoked by the hotbed effect of atmosphere, as a result of the increase of carbonic acid concentration of volcanic origin (BUDYKO, 1981).

A change in the salinity of sea-waters became apparant only in Boreal basins (ZAKHAROV, NAIDIN, TEISS, 1975). The Iranian-Japanese Research Group (1981) consider the low contents of boron and lithium in the Dorashamian sediments of Central Iran to be a result of the fresh-water influence of the restricted lagoon in the Western Tethys. But it is not confirmed by data on carbon isotopic composition of the Midian and Dzhulfian brachiopod shells of Trans-Caucasus (ZAKHAROV, IGNATYEV, KHUDOLOZHKIN, in press). A considerable decrease of oxygen concentration in the atmosphere (ODUM, 1975; BUDYKO, 1981) also seemed to affect considerably the vital activity of organisms by the end of the Permian and early Triassic. In periods of a climatic optimum during the late Permian (synchronous with transgressions), when a taxonomic diversity of marine organisms increased and their interspecific competition intensified, the formation of communities seems to have occured under the existing conditions of K-selection. The early Induan transgression, on the contrary, did not lead to the development of diverse faunas, obviously in connection with the extreme environments of the Permian-Triassic boundary. All groups of the early Induan organisms are characterized by a very low species abundance and equalization of individuals among species. Thus, the fauna of the early Induan apparently developed under the pressure of re-selection. At the same time, owing to the climatic optimum, this fauna became world-wide.

References

BANDO, Y. (1979): Upper Permian and Lower Triassic ammonoids from Abadeh, Central Iran. – Mem. Fac. Educ., Kagawa Univ., pt. *11*, n. 2, 103–138.

BUDYKO, M. I. (1981): Change of surroundings and forming of successive faunas. – Paleont. Zh., n. *4*, 3–11 (in Russian).

CLEMENTS, F. E. (1916): Plant succession of the development of vegetation – Carnegie Institute of Washington Publication, *242*, 512 p.

CLEMENTS, F. E. (1936): Nature and structure of the climax. – Journ. of Ecology, *24*, 252–284.

DOTT, R. H., BATTEM, R. L. (1976): Evolution of the Earth. McGraw Hill Book Company, 504 p.

GULIYEV, R. G., DZHABRAILOV, M. S., ZEYNALOV, M. B. & SHISHAKOV, V. B. (1972): Distribution of bauxitic rocks in the Northwestern part of the Sharuro-Dzhulfa anticlinorium in the Lesser Caucasus. – Dokl. Akad. Nauk SSSR, *206*, 25–27 (in Russian).

Iranian-Japanese Research Group (1981): The Permian and Lower Triassic Systems in Abadeh Region, Central Iran. – Mem. Fac. Sci., Kyoto Univ., ser. Geol., Miner., *47*, n.2, 61–133.

KOTLJAR, G. V., ZAKHAROV, Yu. D., KOCZYRKEVICZ, B. V., KROPATCHEVA, G. S., ROSTOVCEV, K. O., CHEDIJA, I. O. & VUKS, G. P.: Late Permian stage of biological evolution (Dzhulfian and Dorashamian stages of USSR). Nauka, Leningrad, in press (in Russian).

KRASSILOV, V A. (1969): The types of floral successions and their reasons. – Paleont. Zh., n. *3*, 7–23 (in Russian).

KRASSILOV, V. A. (1970): Palaeoecosystems. – Izv. Akad. Nauk SSSR, Ser. Geol., n. *4*, 114–150 (in Russian).

KRASSILOV, V A. (1977): Evolution and biostratigraphy. Nauka, 256 p., Moskva (in Russian).

MARGALEF, R. (1968): Perspectives in ecological theory. Univ. Chicago Press, Chicago, 112 p.

MEIEN, S. V (1971): From the history of the floral dynasties. Nauka, 223 p., Moskva (in Russian).

OCHEV, V G. (1960): About the climate of south-east European part of USSR during Triassic. – Izv. Vysshikh Utchebnykh Zavedenij. Geol. i Razvedka, n. *6*, 18–22.

OCHEV, V. G. (1973): Change peculiarities of the terrestrial vertebrate fauna in the Permian-Triassic boundary. – Bull. Mosk. Obsch. Isp. Prir., Otd. Geol., *48*, n. 1, 70–81 (in Russian).

OCHEV, V G. (1981): On some kinds of the biostratigraphical boundaries (as examplified by the lower tetrapods). In V. A. KRASSILOV and N. I. BLOKHINA (eds.). Ecosystems in stratigraphy, 92–97, Vladivostok (in Russian).

ODUM, E. (1975): Fundamentals of ecology. Publishing House Mir, 740 p., Moskva (in Russian).

RUZHENCEV, V E., T. G. SARYCHEVA (1965): Development and change of marine organisms at the Palaeozoic-Mesozoic boundary. – Trudy Palaeont. Inst. Akad. Nauk SSSR, *108*, 431 p. (in Russian).

SYOMKIN, B. I. (1972): General principles of the introduction of the distinction resemblance and diversity measures in biocenology. – Symposium "Principles and methods of the experimental study of the plant associations" Theses of the papers and speeches. Nauka, 14–16, Leningrad (in Russian).

VAKHRAMEEV, V A., DOBRUSKINA, I. A., ZAKLINSKAJA, E. D., MEIEN, S. V (1970): Palaeozoic and Mesozoic floras of Eurasia and phytogeography of that time. – Trudy Geol. Inst. Akad. Nauk SSSR, *208*, 426 p. (in Russian).

VALENTINE, J. W. (1969): Patterns of taxonomic and ecological structure of the shelf benthos during Phanerozoic time. – Palaeontology, *12*, pt. 4, 684–709.

WTAERHOUSE, J. B. (1976): World correlation for Permian marine faunas. – Pap. Depart. Geol., Univ. Queensland, *7*, n. 2, 232 p.

ZAKHAROV, Yu. D. (1974): The importance of palaeobiogeographical data for the solution of the problem on the Lower Triassic division. – Schrift. Erdwiss. Komm. Österr. Akad. Wiss., *2*, 237–243, Wien.

ZAKHAROV, Yu. D. (1978): Lower Triassic ammonoids of East USSR. Nauka, 224 p., Moskva (in Russian).

ZAKHAROV, Yu. D., NIAIDIN, D. P. & TEISS, R. V (1975): $0^{18}/0^{16}$ rations of Lower Triassic cephalopods of Arctic Siberia and salinity of Boreal basin in

early Mesozoic. – Izv. Akd. Nauk SSSR, Ser. Geol., n. *4*, 101–113 (in Russian).
Zhao, J., Liang, X., Zheng, Z. (1978): The Late Permian cephalopods of South China. – Palaeont. Sinica, new ser. B., n. *12*, 194 p.

A contribution to Project n. 4 (Triassic of the Tethys Realm) and Project n. 106 (Permo-Triassic stage of geological evolution) of the International Geological Correlation Programme (IGCP).

Table 1: Change of dominants within late Permian and early Triassic palaeosuccession of Transcaucasus.

Phase	Stage	Zone, beds	Foraminifers					Tetracorals				
			N	S	d	K	Dominant	N	S	d	K	Dominant
5	–	*Oph.*	0	0	0	0	–	0	0	–	–	–
4	–	*Par.*	48	(0)* 12	6,5	18,8	*Neo.* *St.*	577	(0)* 9	2,9	39,6	*Uf. d.*
3	f	*Sh.*	0	(0)* 0	0	0	–	3?	(2)* 3?	4,2	0	Rare specimens
	e	*Dz.*	10	(0)* 1	0	0	*Neo.*	28?	(2)* 2?	0,7?	92,9?	?
	d	*Ir.*	0	(0)* 0	0	0	–	2?	(2)* 2?	3,3	0	Rare specimens
	c	*Ph.*	44	(0)* 8	4,3	20,5	*Lin.*	4	(0)* 3	3,3	25,0	
2	b	*Ved.*	253	(3)* 19	7,5	39,1	*Rei.*	273	(0)* 10	3,7	37,7	*P. d.* *Pen. l.*
	a	*Ar.*	76	(6)* 13	6,4	11,8	*Nod.*	264	(5)* 12	4,5	93,3	
1	–	*Cod.*	1155	(4)* 104	33,6	8,6	*Cod.*	333	(7)* 12	4,4	46,0	

Designation. N = the conditional index of the quantity (number of the discovered specimens); the index of the rare finds of the microfauna species is accepted conditionally as 1, the index of the frequent microfauna species as 10, very frequent microfauna species as 100; S = quantity of species, $d = \frac{S-1}{\log N}$ = species abundance; K = Fmax – Fmin = index of the degree of equalization for distribution of individuals between

Phase	Stage	Zone, beds	Brachiopods					Nautiloids				
			N	S	d	K	Dominant	N	S	d	K	Dominant
5	–	*Oph.*	0	0	0	0	–	1	1	0	0	Rare specimens
4	–	*Par.*	19	(0)* 9	6,3	26,3		35	(0)* 15	9,1	17,1	*L. l.* *N. sp.*
3	f	*Sh.*	5	(1)* 1	0	0	*Ar. m.*	0	(0)* 0	0	0	–
	e	*Dz.*	14	(1)* 1	0	0		1	(0)* 1	0	0	Rare specimens
	d	*Ir.*	5	(1)* 1	0	0	Rare specimens	0	(0)* 0	0	0	–
	c	*Ph.*	13	(1)* 3	1,8	46,2	*C. t.*	16	(0)* 7	5,0	25,0	Rare specimens
2	b	*Ved.*	>1524	(1)* 27	8,2	22,9	*H. t.* *St. a.*	59	(3)* 24	13,0	18,6	
	a	*Ar.*	>3324	(12)* 28	7,6	19,5	*Ar. l.* *Ar. q.*	366	(18)* 40	15,2	20,5	*N. m.*
1	–	*Cod.*	>1976	(17)* 27	7,9	20,9	*Ar. i.* *C. d.*	1	(1)* 1	0	0	

species (Fmax = occurence frequency of the dominant species, Fmin = occurence frequency of the most scanty species. The sign* indicates the number of species in common between adjacent zones. Dominants: *Cod.* = *Codonofusiella*, *Nod.* = *Nodosaria*, *Rei.* = *Reichelina*, *Lin.* = *Lingulina*, *Neo.* = *Neoendothyra*, *St.* = *Streblospira*, *P. d.* = *Pentaphyllum dzhulfense* (ILJINA), *Pen. l.* = *Pentamplexus leptoconicus* (ABICH), *Uf. d.* = *Ufimia differentiata* (ILJINA), *Ar. i.* = *Araxilevis intermedius* (ABICH), *C. d.* = *Compressoproductus djulfensis* (STOYANOW), *Ar. l.* = *Araxathyris lata* (GRUNT), *A. qu.* = *Araxathyris quadrilobata* (ABICH),

Phase	Stage	Zone, beds	Ammonoids					Ostracodes				
			N	S	d	K	Dominant	N	S	d	K	Dominant
5	–	*Oph.*	130	3	1,0	0	*Oph. m.*	0	0	0	0	–
4	–	*Par.*	358	(0)* 14	5,1	17,1	*Par. v.*	13	(0)* 4	2,7	69,2	*C. i.*
3	f	*Sh.*	122	(7)* 11	4,8	50,0	*Sh. sh.*	7	(3)* 7	7,1	0	Rare specimens
	e	*Dz.*	57	(4)* 6	2,8	68,4	*Dz. s.*	17	(6)* 17	13,1	0	?
	d	*Ir.*	98	(2)* 6	2,5	42,9	*Ir. t.*	6	(5)* 6	6,4	0	Rare specimens
	c	*Ph.*	214	(2)* 10	3,9	33,2	*X. a.*	76	(4)* 22	11,1	11,8	*F. h.* *F. s.* *B. a.*
2	b	*Ved.*	179	(2)* 21	8,9	19,6	*Ps. a.*	46	(11)* 24	13,8	19,6	*F. h.* *F. o.* *B. ?s.*
	a	*Ar.*	401	(7)* 33	12,3	32,7		19	(18)* 19	14,1	0	?
1	–	*Cod.*	4	(2)* 2	1,7	50,0	Rare specimens	24	(11)* 24	16,7	0	?

H. t. = *Haydenella tumida* (WAAGEN), *St. a.* = *Stenoscisma armenicum* SOKOLSKAJA, *C. t.* = *Comelicania triangularis* GRUNT, *N. m.* = *Neocycloceras lopingense* (STOYANOW), *N. sp.* = *Neocycloceras* sp., *Ps. a.* = *Pseudogastrioceras abichianum* (MÖLLER), *X. a.* = *Xenodiscus araxensis* SHEVYREV, *Ir. t.* = *Iranites transcaucasius* (SHEVYREV), *Dz. s.* = *Dzhulfites spinosus* SHEVYREV, *Sh. sh.* = *Shevyrevites shevyrevi* TEICHERT et KUMMEL, *Par. v.* = *Paratirolites vediensis* SHEVYREV, *Oph. m.* = *Ophiceras (Lytophiceras) medium* GRIESBACH. Designation of the zones as in Fig. 1.

Table 2: Calculation of the distinction degree of the phases and stages of Trans-Caucasian succession during the time of Permian-Triassic boundary on the species level with the registration of the quantity.

1. Foraminifers

Oph.	*Par.*	*Sh.*	*Dz.*	*Ir.*	*Ph.*	*Ved.*	*Ar.*	*Cod.*	Zone
0*)	100	100	100	100	100	100	100	100[1])	*Oph.*
	12	100	96,6	100	91,3	96	79,0	97,5	*Par.*
		0	100	100	100	100	100	100	*Sh.*
			1	100	100	100	100	100	*Dz.*
				0	100	100	100	100	*Ir.*
					8	98,0	95,0	97,9	*Ph.*
						19	97,6	97,9	*Ved.*
							13	97,9	*Ar.*
								104	*Cod.*

2. Tetracorals

Oph.	*Par.*	*Sh.*	*Dz.*	*Ir.*	*Ph.*	*Ved.*	*Ar.*	*Cod.*	Zone
0*)	100	100	100	100	100	100	100	100[1])	*Oph.*
	9	99,3?	98,3?	99,3?	100	60,0	57,9	54,7	*Par.*
		3?	87,1?	20,0?	71,4	99,3	98,5	99,4	*Sh.*
			2?	86,7?	100	99,3	89,7	99,4	*Dz.*
				2?	100	99,3	98,5	99,4	*Ir.*
					3	100	100	100	*Ph.*
						10	41,2	43,6	*Ved.*
							12	20,6	*Ar.*
								12	*Cod.*

3. Brachiopods

Oph.	*Par.*	*Sh.*	*Dz.*	*Ir.*	*Ph.*	*Ved.*	*Ar.*	*Cod.*	Zone
0*)	100	100	100	100	100	100	100	100[1])	*Oph.*
	9	58,3	63,6	58,3	54,5	98,6	99,8	99,8	*Par.*
		1	47,4	100	44,4	99,3	99,9	100	*Sh.*
			1	47,4	63,0	98,2	99,9	100	*Dz.*
				1	64,3	99,3	99,9	100	*Ir.*
					3	99,4	99,9	100	*Ph.*
						27	89,4	82,3	*Ved.*
							28	57,0	*Ar.*
								27	*Cod.*

4. Nautiloids

Oph.	*Par.*	*Sh.*	*Dz.*	*Ir.*	*Ph.*	*Ved.*	*Ar.*	*Cod.*	Zone
1*)	100	100	100	100	100	100	100	100[1])	*Oph.*
	15	100	93,9	100	43,7	98,1	95,3	100	*Par.*
		0	100	100	100	100	100	100	*Sh.*
			1	100	92,6	99,9	99,9	100	*Dz.*
				0	100	100	100	100	*Ir.*
					7	99,7	99,5	100	*Ph.*
						24	98,0	100	*Ved.*
							40	100	*Ar.*
								1	*Cod.*

5. Ammonoids

Oph.	*Par.*	*Sh.*	*Dz.*	*Ir.*	*Ph.*	*Ved.*	*Ar.*	*Cod.*	Zone
3*)	100	100	100	100	100	100	100	100[1])	*Oph.*
	14	86,2	94,2	98,7	97,2	98,9	99,2	98,3	*Par.*
		11	85,5	94,5	95,2	97,3	99,2	96,9	*Sh.*
			6	94,8	96,4	99,2	99,6	96,7	*Dz.*
				6	92,9	92,1	96,0	94,1	*Ir.*
					10	90,3	94,1	97,2	*Ph.*
						21	82,1	96,7	*Ved.*
							33	98,0	*Ar.*
								2	*Cod.*

6. Ostracodes

Oph.	*Par.*	*Sh.*	*Dz.*	*Ir.*	*Ph.*	*Ved.*	*Ar.*	*Cod.*	Zone
0*)	100	100	100	100	100	100	100	100[1])	*Oph.*
	4	70,0	80,0	78,9	93,2	89,8	81,2	92,6	*Par.*
		7	50,0	53,8	83,1	77,4	61,5	87,1	*Sh.*
			17	56,5	69,9	65,1	50,0	65,9	*Dz.*
				6	90,2	88,5	76,0	86,7	*Ir.*
					22	67,2	78,9	88,0	*Ph.*
						24	44,6	65,7	*Ved.*
							19	48,8	*Ar.*
								24	*Cod.*

*) Number of species.
[1]) The distinction degree (1-Ko).

$$1\text{-Ko} = \left(1 - \frac{2\,m(X_1\,X_2)}{m(X_1) + m(X_2)}\right) \cdot 100\ \%$$ (SYOMKIN, 1972; ZAKHAROV, 1974, 1978).

Designation as in Fig. 1.

Table 3: Number of invertebrate species of Upper Permian and Lower Triassic of Iran and China

Palaeosuccession phase	Trans-Caucasus scale		Central Iran							South China							
	Stage	Zone	Formation	Zone	Foraminifers	Brachiopods	Bivalves	Nautiloids	Ammonoids	Formation	Zone	Foraminifers	Corals	Brachiopods	Bivalves	Nautiloids	Ammonoids
5	In-duan	*Oph.*		*Cl.*	0	0	5	0	7		*O.w. -Cl.*	0	0	?	5	0	4
4	Dorashamian	*Par*	Hambast	*P. P.-Sh.*	0	3	0	2	14	Changxing	*R. P.-Pl. Ps.-T.*	10	9	>19	17	12	83
3		*Sh. Dz. Ir. Ph.*		*Sh.*	1	2	0	0	6		*„P."-Sh. Ir.-Ph.*	16	0	6	8	0	5
2	Dzhulfian	*Ved.*		*V. n.*	1	5	0	4	14	Wujiaping	*San.*	2	0	?	13	0	7
		Ar.		*Ar. t.*	7	4	0	7	14		*Ar.-K. An.-P.*	8	2	39?	17	4	54
1	Midian	*Cod.*		*„Arl."*	20	14	0	2	1		–	?		?			?
			Abadeh 5	*C. k.*	24	1	0	0	0		Litoral-continental conditions						
			Abadeh 4	*Sph.*	52	11	4	0	2								

Designation of the zones: *Sph.* = *Sphaerulina* sp., *C. k.* = *Codonofusiella kwangsiana*, *„Arl."* = *Araxilevis* beds, *Ar. t.* = *Araxoceras tectum* subzone, *V. n.* = *Vedioceras nakamurai*, *Sh.* = *Shevyrevites*, *P.-Sh.* = *Shevyrevites-Paratirolites*, *P.* = *Paratirolites*, *Cl.* = *Claraia* beds, *An.-P.* = *Anderssonoceras-Prototoceras*, *Ar.-K.* = *Araxoceras-Konglingites*, *San.* = *Sanyangites*, *Ir.-Ph.* = *Iranites? – Physonites?*, *„P."-Sh.* = *„Paratirolites"-Shevyrevites*, *Ps.-T.* = *Pseudostephanites – Tapashanites*, *P.-Pl.* = *Pseudotirolites – Pleuronodoceras*, *R.* = *Rotodiscoceras*, *O. w.-Cl.* = *Otoceras* cf. *woodwardi* beds and *Claraia* beds. Other designation as in Fig. 1.

Zeitschrift/Journal: Sitzungsberichte der Akademie der Wissenschaften mathematisch-naturwissenschaftliche Klasse

Jahr/Year: 1983

Band/Volume: 192

Autor(en)/Author(s): Zakharov Yuri D.

Artikel/Article: Palaeosuccessions and the Basic Factors of Syngenesis During the Time of the Permian-Triassic Boundary. 37-58