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Global changes

Evolution of the biosphere

Changes in the Taxonomic and Ecologic Composition of Shelf Benthic Assemblages at the Permian–Triassic Boundary

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Abstract – Changes in the taxonomic and ecologic composition of shelf benthic assemblages at the Permian–Triassic boundary and their possible causes were studied. Analysis of the data available showed that though the mass extinction and general crisis of the biota at this boundary were among the most considerable of Phanerozoic events, they were, among benthic groups, neither synchronous nor similar in scale. Ethological and trophic compositions were stable in most shelf zones; only reef assemblages composed of sessile sestonophagi disappeared.

At the beginning of the Permian the following benthic groups dominated the shelves: foraminifers, tetracorals, tabulates, brachiopods (Spiriferida and Productida), typical Paleozoic bryozoans, namely Trepostomida, Cystoporida, Fenestellida, Cryptostomida, Rhabdomesida, crinoids, and ostracodes. Bivalve mollusks, gastropods, and sponges also occurred, as well as hyolithids, echinoderms (Blastoidea, Echinida, Holothurioidea, Asteroidea, and Ophiuroidea), hydroids, rostroconchs, trilobites, and other rare groups.

In the second half of the Permian, the extinction of some groups began (Fig. 1), and by the end of the Permian it resulted in the disappearance of fusulinids, hyolithids, blastoids, edrioasteroids, trilobites, and brachiopods, namely Orthida, Strophomenida, and Productida. However, athyrids, rhynchonellids, and terebratulids became dominant. The Bryozoan orders Fenestellida, Cryptostomida, and Rhabdomesida disappeared, and only four trepostomid genera survived into the Triassic. Paleozoic crinoids Flexibilia, Camerata, and most of Inadunata, as well as echinoid orders Palaechinoida and Echinocystitoida became extinct, conularians and tabulates almost disappeared (Morozova, 1970; Dobruskina, 1976; Krasilova, 1979; Raup, 1979; Shimanskii, 1987; Stanley, 1988; Kotlyar and Rostovtsev, 1989; and others).

The late Permian extinction maximum, the same as that of the Maestrichtian, was one of the greatest in the Phanerozoic: more than 90% of species, 65 - 76% of genera, and 52 - 57% of families became extinct (Raup, 1978, 1979; Sepkoski, 1978, 1979, 1986). However, the extinction was not catastrophic. Rather, it had a selective character.

Among the extinct forms, the polyhaline thermophilic groups, especially representatives of reef assemblages, dominated (Fisher, 1968; Dagys and Ustritsky, 1973; Gobbett, 1973; Kozur, 1980; Ross and Ross, 1982; Flügel and Stanley, 1984; and others). Before their disappearance, the latter usually occurred in basins of the tropical region, including the Paleotethys (Kozur, 1980; Stanley, 1988). Such forms were fusulinids (Foraminifera), tetracorals, and many bryozoans. Late Permian reefs were mainly formed by sponges and calcareous algae (Flügel and Stanley, 1984).

Different authors suggested the following causes of the late Permian extinction: (1) a decrease in ocean water salinity, up to 30 or 31.5‰, as a result of regression and brine concentration in the abyssal areas (Fischer, 1964, 1968, 1986; Lantzy *et al.*, 1977; Stevens, 1977; Zharkov, 1981); (2) reduction of the area of epicontinental seas because of regression (Valentine and Moore, 1972; Schopf, 1974; Simberloff, 1974; Kozur, 1980; Hallam, 1989), which resulted in the disappearance of certain ecologic niches, including reef knolls (*Razvitie i Smena* ..., 1965; Boukot, 1975); (3) "oxygen" water mixing after a cool period associated with upwelling (Wilde and Berry, 1986); (4) global cooling and glaciation in the southern polar region and, to a lesser extent, in North Siberia, as well as a 125 - 225 m drop in the eustatic sea level, which caused the disappearance of warm shallow seas (Hallam, 1984; Stanley, 1988); (5) an increase in nutrient deficiency in sea water because of the accumulation of sediments rich in organic matter that, in turn, resulted in a lowering of the oxygen content in the atmosphere and the extinction of land plants and animals (Hoffman, 1989); (6) a decrease in phytoplankton (Tappan, 1982); or (7) combinations of the above-mentioned factors (Astaf'eva-Urbaitis and Yasamanov, 1986). Other hypotheses have also been suggested, e.g., a cosmic one (Schindewolf, 1954; McLaren, 1970), a reduction of genetic variability (Bretsky and Lorenz, 1970), change in the oxygen content (McAlester, 1970, 1971), and an increase of arid and continental areas (Nakazawa, 1985).

Most of these hypotheses are common nowadays, and there is no consensus on the causes of extinction.

The duration and rate of the late Permian extinction are also open to discussion. According to S. Stanley (1988), the extinction occurred throughout the late Permian, i.e., during the Guadalupian and Dzhulfian (about 10 Ma), whereas, according to G.V. Kotlyar and K.O. Rostovtsev (1989), extinction took place only in the second half of the late Permian, and in the first half – during the Kubergandian and Midian – all faunal groups, including higher fusulinids, flourished. The extinction rate was not catastrophic, but rather was gradual and irregular, so that some Permian relics still occurred in the early Triassic seas (*Razvitie i Smena* ..., 1965; Stepanov, 1972; Dagys, 1974; Kozur, 1980; Tappan, 1982; Kotlyar *et al.*, 1983; Clark *et al.*, 1986; Passini, 1988; Kotlyar and Rostovtsev, 1989).

The late Permian extinction considerably impoverished the benthos. At the beginning of the Triassic, only bivalve mollusks dominated, whereas small foraminifers, brachiopods, gastropods, bryozoans, sphinctozoans, echinoderms, and crustaceans were scarce. Rare corals, most likely, also occurred, and later became widespread (Fig. 1).

The early Triassic fauna was cosmopolitan and contained many relict Permian genera and species, which survived, within limited areas, the late Permian crisis (*Razvitie i Smena* ..., 1965; Fisher, 1968; Stepanov, 1972; Kummel, 1973; Dagys, 1974; Dobruskina, 1976; Boukot, 1975; Krasilova, 1979; Shimanskii, 1987; Kotlyar and Rostovtsev, 1989).

The diversity of benthos began to increase only during the second half of the early Triassic, during the Olenekian. In the middle Triassic, scleractinians appeared, as well as some new taxa of small foraminifers, brachiopods, gastropods, crinoids, and other groups. Part of the new faunal elements were formed from the Permian euryhaline fauna relics preserved in refugia, shallow semisea late Permian basins (Fischer, 1964, 1968; Stepanov, 1972; Kozur, 1980), and the other parts, from cosmopolitan early Triassic forms.

As for the Permian and Triassic benthic assemblages composition in different biogeographic areas, the assemblages of the tropical region, especially reefs, were characterized by the greatest taxonomic diversity.

In the Permian, brachiopods, bivalve mollusks, and bryozoans dominated in marginal sea areas (littoral and

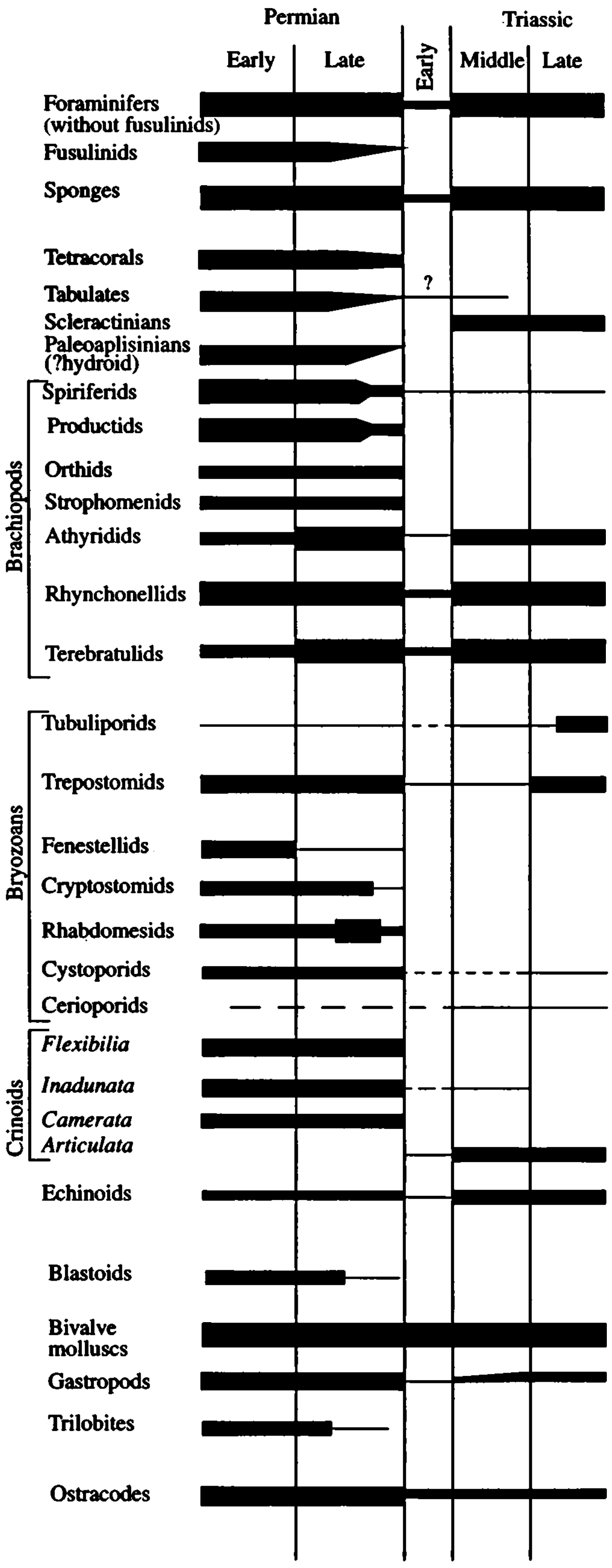

Fig. 1. Distribution of the main invertebrate groups that composed benthic shelf assemblages in the Permian and Triassic.

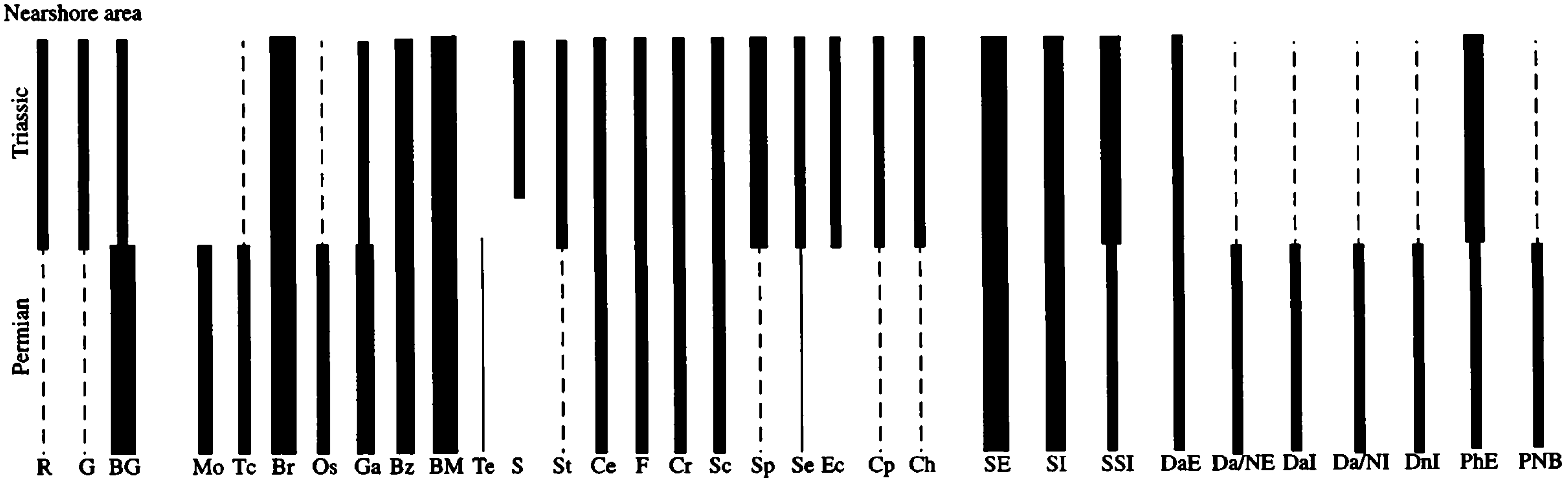

Fig. 2. Taxonomic and ethologotrophic composition of benthic assemblages from the nearshore areas of Permian and Triassic seas. Taxonomic groups: BG – blue-green algae; Bl –blastoids; BM – bivalve mollusks; Br – brachiopods; Bz – bryozoans; Ce – cephalopods; Ch – chaetetids; Co – conodonts; Con – conulariids; Cp – cirripeds and other crustaceans; Cr – crinoids; Ec – echinoids; F – foraminifers; G – green algae; Ga – gastropods; Hy – hydroids; Mo – monoplacophorans; Os – ostracodes; Pa – paleoaplisinians (? hydroid); Pr – problematics; R – red algae; S – scleractinians; Sc – scaphopods; Se – serpulids; Sp – sponges; St – stromatoporids; Ta – tabulates; Tc – traces; Te – tetracorals; Tr – trilobites. Ethologotrophic groups: DnI – infaunal nonassorting detritophagi; DaI – infaunal assorting detritophagi; Da/NI – infaunal assorting detritophagi/necrophagi; Da/NE – epifaunal assorting detritophagi/necrophagi; DaE – epifaunal assorting detritophagi; SI – infaunal sestonophagi; SSI – semi-infaunal; SE – epifaunal sestonophagi; PhE – epifaunal phytophagi; PNB – nektobenthic predators; PE – epifaunal predators.

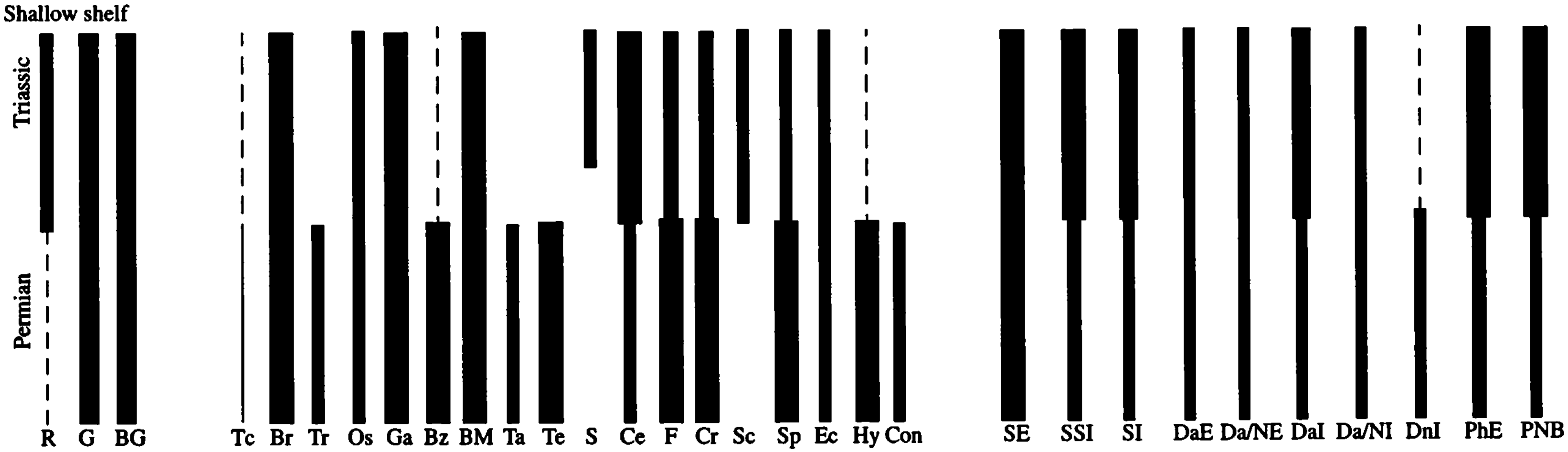

Fig. 3. Taxonomic and ethologotrophic composition of benthic assemblages from the shallow shelf of Permian and Triassic seas. Legend is the same as for Fig. 2.

lagoons) and in the nearshore shallow basins of this region. Foraminifers, gastropods, scaphopods, monoplacophorans, ostracodes, crinoids, ? worms, rare tetracorals, and nektobenthic cephalopods also occurred there. Epifaunal sestonophagi (vagile and sessile, and free-lying) dominated, whereas infaunal sestonophagi and detritophagi, epifaunal mobile phytophagi, detritophagi and necrophagi, as well as nektobenthic predators were of minor importance (Fig. 2).

On the open shallow shelf, the benthos was considerably more diverse. It included numerous brachiopods, bryozoans, foraminifers, tetracorals, hydroids, crinoids, sponges, gastropods, and bivalve mollusks, as well as rarer tabulates, trilobites, echinoids, ostracodes, and nektobenthic cephalopods. Among the ethologotrophic groups, the epifaunal sestonophagi were dominant, whereas semi-infaunal and infaunal sestonophagi, epifaunal mobile detritophagi, necrophagi, phytophagi, and nektobenthic predators were less important (Fig. 3).

Bioherms were formed on the shallow shelf sandbanks by bryozoans, tetracorals, hydroids, sphinctozoans and sclerosponges, some brachiopods, and bivalve mollusks, as well as by calcareous algae (green, blue-green, and red). Numerous foraminifers, crinoids, gastropods, common monoplacophorans, scaphopods, tabulates, ostracodes, blastoids, and serpulids were associated with the bioherms (Fig. 4).

On the deep-water shelf, benthic forms were less diverse and numerous. This sea zone was inhabited by foraminifers, bryozoans, sponges (usually siliceous), infaunal bivalve mollusks, gastropods, ostracodes, nektobenthic cephalopods, and, more seldom, by other groups. Ethologotrophic composition was rather mixed, but no one group prevailed. Some epifaunal sessile and free-lying sestonophagi, mobile detritophagi, and necrophagi, infaunal detritophagi, (?) planktobenthic sestonophagi, and nektobenthic predators were recorded there (Fig. 5).

In the marginal, nearshore shallow sea areas of the boreal and notal regions, bivalve mollusks were dominant. Gastropods, brachiopods, and bryozoans were common, whereas other groups were relatively few. Blue-green calcareous algae were widespread. Epifaunal sestonophagi prevailed. On the shallow shelf, brachiopods, bryozoans, crinoids, and foraminifers, which dominated in the assemblages of the tropical region, were supplemented with bivalve mollusks and gastropods. Tetracorals were scarcer than in the tropical region, whereas hydroids were absent. The same as in the above-mentioned zones, epifaunal sestonophagi, vagile and sessile, as well as free-lying, prevailed. Semi-infaunal and infaunal sestonophagi, epifaunal and infaunal mobile detritophagi, and necrophagi, phytophagi, and nektobenthic predators were rarer.

In both the Triassic and Permian, the greatest taxonomic diversity characterized assemblages of the tropical biogeographic region, especially reefs. Reefs and other bioherms were formed during the middle Triassic by scleractinians, calcisponges, hydroids, forms of obscure origin (*Tubiphytes*, *Thaumatoporella*, and *Ladinella*), and calcareous algae. Bivalve mollusks, brachiopods, bryozoans, foraminifers, and other groups occurred within the reefs. They were referred to different ethologotrophic groups, namely to epifaunal vagile and free-lying sestonophagi, epifaunal mobile detritophagi and necrophagi, phytophagi, nektobenthic predators and necrophagi, scarcer infaunal detritophagi and sestonophagi, and semi-infaunal sestonophagi (Fig. 4). At the same time, the epifaunal sessile sestonophagi were predominant in the reef assemblages.

Bivalve mollusks dominated in the rest of the shelf zones of the tropical and boreal regions. Brachiopods and gastropods were also widespread, especially in shallow water. Conchostracans usually inhabited nearshore areas, whereas other invertebrate groups, namely foraminifers, sponges, scleractinians, bryozoans, scaphopods, echinoderms, and serpulids were of secondary importance.

The shallow shelf and nearshore areas were dominated by epifaunal vagile (more seldom free-lying) sestonophagi. Numerous phytophagi and semi-infaunal sestonophagi were present, whereas infaunal sestonophagi, infaunal and epifaunal detritophagi and necrophagi, as well as nektobenthic predators and necrophagi were considerably less abundant (Figs. 2 and 3).

Bivalve mollusks were dominant in deep-water assemblages. Scleractinians, brachiopods, gastropods, scaphopods, crinoids, and echinoids were considerably rarer.

The deep-water shelf was inhabited equally by semi-infaunal (? or pseudoplanktonic) and epifaunal vagile sestonophagi, infaunal detritophagi, and nektobenthic predators and necrophagi. Infaunal sestonophagi, as well as epifaunal detritophagi and predators were scarce (Fig. 5).

Accordingly, though mass extinction and crisis of the biota at the Permian–Triassic boundary were among the major Phanerozoic events, they were not synchronous for all the organisms. Different groups became extinct at different times, and the number and diversity of some of them decreased throughout the late Permian or its second half. The dimensions of the extinction were also unequal among different groups.

The ethologotrophic composition was stable on most of the shelf. Only the taxa characteristic of different ecologic groups were replaced.

Only the areas with reef structures in the tropical biogeographic region were marked by considerable changes as a result of the extinction of main reef-constructing organisms, so that at the beginning of the Triassic, reef assemblages almost disappeared and were formed again only at the middle Triassic. As much as reef-constructing forms were represented mainly by sessile sestonophagi, just that ethologotrophic group suffered most from the crisis.

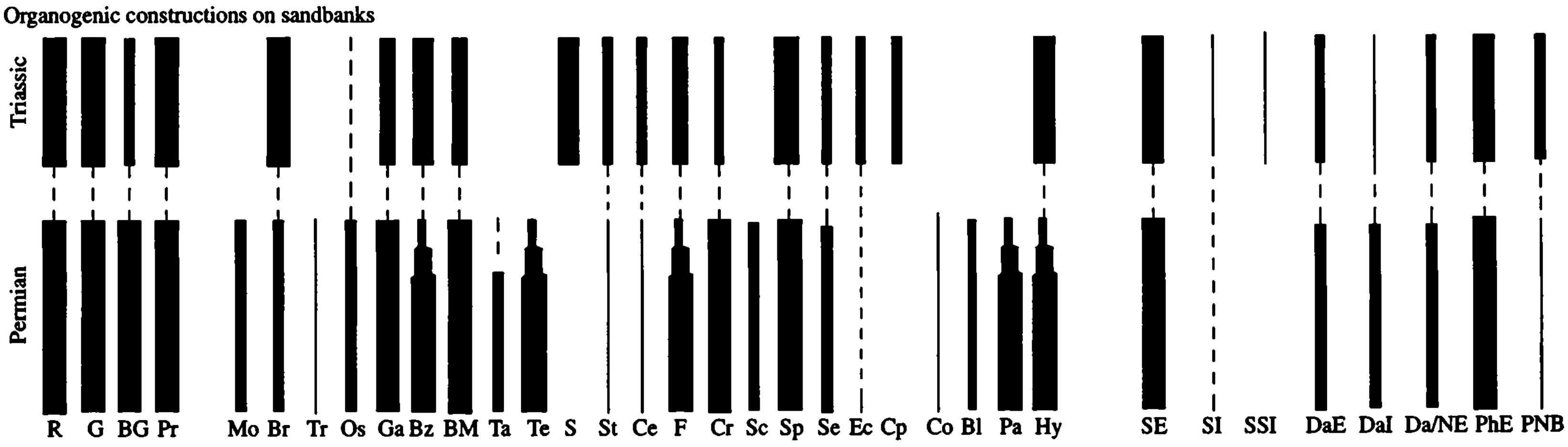

Fig. 4. Taxonomic and ethologotrophic composition of benthic assemblages of organogenic constructions on sandbanks of the Permian and Triassic seas. Legend is the same as for Fig. 2.

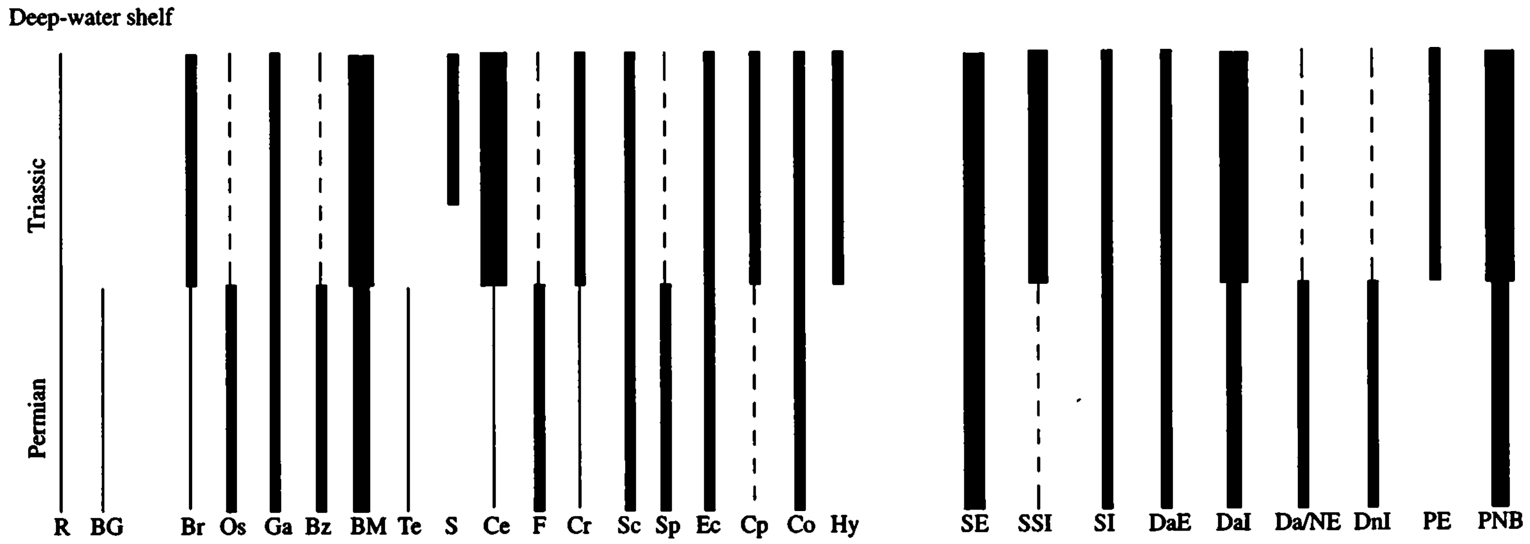

Fig. 5. Taxonomic and ethologotrophic composition of benthic assemblages from the deep-water shelf of the Permian and Triassic seas. Legend is the same as for Fig. 2.

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