

# Differentiation of Foraminiferal Assemblages and Dynamics of Their Taxonomic Diversification in the Jurassic

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**Abstract**—Data on Jurassic foraminifers from key localities in continents and oceans is analyzed. Their distribution range spans the stratigraphic interval from the Aalenian to the Tithonian equal to 32 million years. Among 23 localities (including 7 Jurassic sections recovered by deep sea drilling), data for 9 are originally obtained. Information on other localities is presented on the basis of published data. The assemblages studied comprise three types of foraminiferal fauna corresponding to those distinguished by V.A. Basov for different climatic zones: Arctic (cold), Boreal (moderately cold), and Tethyan (warm tropical to subtropical). It is established that faunas different not only in dominant components but also in taxonomic composition of a high rank were characteristic of the Tethyan and Peritethyan regions in the Jurassic. Assemblages of different types are present in adjacent sections and even in the same section. Neither climatic fluctuations nor penetration of cold or warm water masses, as well as fauna migration and invasion, can explain this phenomenon. The mosaic distribution of faunal assemblages and alternation of different fauna types are the result of bathymetric differentiation and related environmental factors such as temperature, type of bottom substrate, hydrodynamics, and distance to the shore line.

**Key words:** *foraminifers, assemblages, differentiation, paleobiogeography, endemic forms, cosmopolitan forms, bathymetric zonation.*

Any stratigraphic and paleobiogeographic study at the stage of generalization implies systematization of data on regularities in the evolution and distribution of the fauna and on factors influencing these subjects.

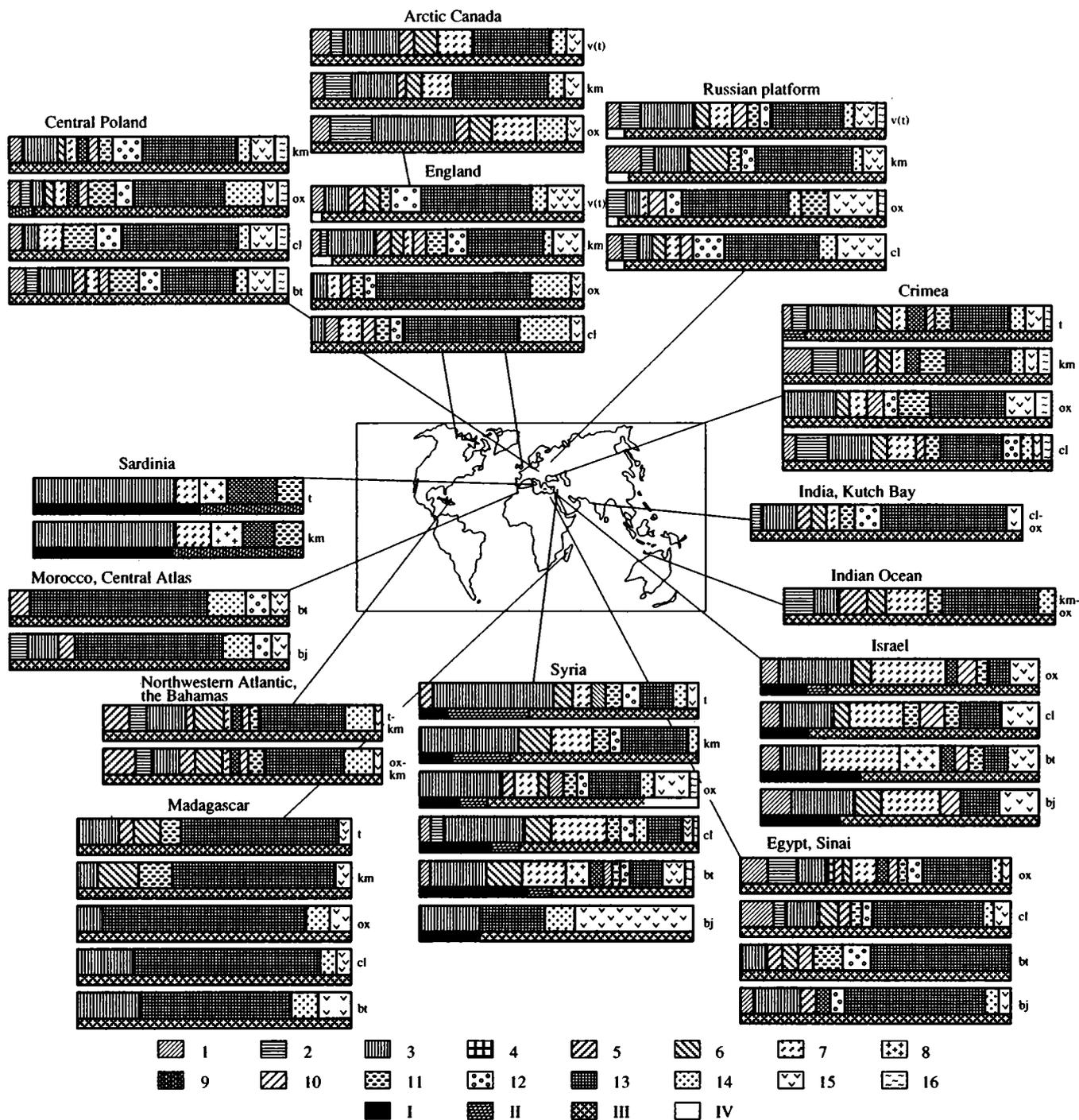
The Jurassic is of great interest in this aspect because of major reorganizations in the geologic history of continents and oceans that happened at that time.

The Jurassic represents the middle part of the Mesozoic; therefore, its fauna retains the peculiar Early Mesozoic (Triassic) features and, accordingly, genetic relations of many groups of organisms with those of preceding epochs. At the same time, it was an epoch of formation of new groups, whose evolution and further development were related to the Cretaceous. All the factors left their imprints on foraminifers, benthic assemblages of which inhabited areas from the Arctic regions to the southern hemisphere and were unique in abundance and diversity during the Mesozoic.

Important information on the Jurassic foraminifers of continents and oceans has been acquired to date. Deep sea drilling supplied us with material that enhanced our understanding of this fauna. Even a general study of the published data shows the marked diversity of the Jurassic foraminiferal assemblages, the variability of their taxonomic composition and structure, and mosaic patterns of their distribution in the Jurassic sedimentary basins (Fig. 1).

Analysis of the composition and data on stratigraphic and paleobiogeographic ranges of the Jurassic foraminifers (Table 1) shows the following.

The foraminiferal assemblages of the studied stratigraphic interval (the Aalenian–Tithonian) are represented exclusively by benthic forms. Planktonic foraminifers (*Eoglobigerina*, *Globuligerina*, and *Conoglobigerina* genera) are rare and represented by 11 species only. These are known from the early Bajocian to the Tithonian inclusive and are confined to the Tethyan, Peritethyan, and Subboreal zones. Planktonic foraminifers were not found in the Arctic regions (Arctic Canada, northern Siberia, and Arctic islands). In some localities (Turkey, the Russian platform, and Crimea), populations of planktonic foraminifers are as abundant as thousands of shells per 50 g of rock. Usually, they are sporadic and represented by single specimens. The foraminiferal assemblages studied comprise 177 genera, which belong to 16 orders. The number of genera in each order is different. More abundant are genera of the Lituolida, Ataxophragmiida, Lagenida, and Rotaliida orders. The dynamics of generic diversification in the Lagenida and Rotaliida orders during the Jurassic is shown in Fig. 2. The comparison of stratigraphic and paleobiogeographic ranges of genera showed that cosmopolitan forms existed longer, as compared to endemic (both Tethyan and Boreal) genera demonstrating narrow stratigraphic intervals rarely exceeding a stage (geologic age).



**Fig. 1.** Taxonomic composition of Jurassic foraminiferal assemblages (by orders, %): Madagascar after Espitalié and Sigal (1963) and Kuznetsova (1976); Syria after Kuznetsova *et al.*, (1996); Israel after Mayne (1966) and Picard and Hirsch (1987); Egypt, Sinai, after Said and Barakat (1958); Morocco, Central Atlas, after Sossipatrova and Rahhali (1974); Riegraf *et al.* (1984); India, Kutch Bay, after Bhalla and Abbas (1978); Indian Ocean, Argo Abyssal Plain, DSDP Leg 27, Site 261, after Kuznetsova (1974); Crimea after Kuznetsova and Gorbachik (1985); Sardinia after Azema *et al.* (1977); Poland after Bielecka (1960), Bielecka and Styk (1968, 1981), and Bielecka and Kuznetsova (1969); England after Cordey (1963) and Kuznetsova (1979); Russian platform after Kuznetsova (1979), Grigyalis (1985), and Azbel' (1989); Arctic Canada after Souaya (1976) and Hedinger (1995); northwestern Atlantic, the Bahamas, DSDP sites 100, 101, 534 after Luterbacher (1972), Gradstein (1978, 1983), and Gradstein and Sheridan (1983). Orders of foraminifera: (1) Astorhizida, (2) Ammodiscida, (3) Lituolida, (4) Rzehakinida, (5) Trochamminida, (6) Textulariida, (7) Ataxophragmiida, (8) Orbitolinida, (9) Involutinida, (10) Cornuspirida, (11) Spirillinida, (12) Miliolida, (13) Lagenida, (14) Polymorphinida, (15) Rotaliida, (16) Globigerinida; (I) Tethyan endemics; (II) Tethyan and Subtethyan forms; (III) Boreal and cosmopolitan forms; (IV) Boreal endemics.

Table 1. Stratigraphic and paleogeographic ranges of the Jurassic foraminifers

Order, genus	J <sub>2</sub> a	J <sub>2</sub> bj	J <sub>2</sub> bt	J <sub>2</sub> cl	J <sub>3</sub> ox	J <sub>3</sub> km	J <sub>3</sub> t(v)
<b>Order Astrorhizida</b>							
<i>Rhizammina</i>							
<i>Saccammina</i>							
<i>Hyperammina</i>							
<i>Bathysiphon</i>							
<i>Lagenammina</i>							
<i>Rhabdammina</i>							
<b>Order Ammodiscida</b>							
<i>Ammodiscus</i>							
<i>Ammodiscoides</i>							
<i>Hemidiscus</i>							
<i>Arenoturrspirillina</i>							
<i>Lituotuba</i>							
<i>Saturnella</i>							
<i>Tolypammina</i>							
<i>Glomospira</i>							
<i>Glomospirella</i>							
<i>Amovertella</i>							
<i>Turritellevella</i>							
<b>Order Lituolida</b>							
<i>Reophax</i>							
<i>Haplophragmoides</i>							
<i>Ammobaculites</i>							
<i>Bulbobaculites</i>							
<i>Ammomarginulina</i>							
<i>Ammoscalaria</i>							
<i>Kutsevella</i>							
<i>Evolutinella</i>							
<i>Flabellammina</i>							
<i>Flabellamminopsis</i>							
<i>Triplasia</i>							
<i>Frankeina</i>							
<i>Nautiloculina</i>							
<i>Phenacophragma</i>							
<i>Stomatostoecha</i>							
<i>Placopsilina</i>							
<i>Acruliammina</i>							
<i>Recurvoides</i>							
<i>Plectorecurvoides</i>							
<i>Cribrostomoides</i>							
<i>Haplophragmium</i>							
<i>Charentia</i>							
<i>Melathrokerion</i>							
<i>Labyrinthina</i>							
<i>Feurtillia</i>							

Table 1. (Contd.)

Order, genus	J <sub>2a</sub>	J <sub>2bj</sub>	J <sub>2bt</sub>	J <sub>2cl</sub>	J <sub>3ox</sub>	J <sub>3km</sub>	J <sub>3t(v)</sub>
<i>Alveosepta</i>					-----	-----	-----
<i>Bramkampella</i>							-----
<i>Pseudocyclammina</i>					-----	-----	-----
<i>Choffatella</i>					-----	-----	-----
<i>Torinosuella</i>					-----	-----	-----
<i>Dhrumella</i>			-----				
<i>Everticyclammina</i>			-----		-----	-----	-----
<i>Amijiella</i>			-----				
<i>Anchispirocyclus</i>					-----	-----	-----
<i>Pseudospirocyclus</i>						-----	-----
<i>Haurania</i>			-----				
<i>Timidonella</i>	-----						
<i>Alzonella</i>	-----						
<i>Limognella</i>	-----						
<i>Flabellocyclolina</i>					-----		
<b>Order Trochamminida</b>							
<i>Eggerella</i>				-----			
<i>Trochammina</i>		-----			-----	-----	-----
<i>Conotrochammina</i>							
<b>Order Textulariida</b>							
<i>Textularia</i>	-----			-----			-----
<i>Spirotextularia</i>				-----			
<i>Spiroplectammina</i>				-----			
<i>Eomarssonella</i>				-----			
<i>Marssonella</i>							-----
<i>Orientalia</i>					-----		
<i>Dorothia</i>					-----		-----
<i>Riyadhella</i>			-----				
<i>Redmondoides</i>			-----				
<i>Riyadhoides</i>			-----				
<i>Pseudomarssonella</i>			-----				
<i>Bigenerina</i>			-----				
<i>Pseudobolivina</i>							-----
<b>Order Ataxophragmiida</b>							
<i>Paleopfenderiuna</i>			-----		-----		
<i>Pfenderella</i>			-----		-----		
<i>Sanderella</i>					-----		
<i>Satorina</i>					-----		
<i>Steinekella</i>					-----		
<i>Praekurnubia</i>			-----				
<i>Kurnubia</i>			-----				-----
<i>Arenovirgulina</i>					-----		
<i>Gaudryina</i>					-----		
<i>Verneuilina</i>					-----		
<i>Verneuilinoidea</i>			-----		-----		-----

Table 1. (Contd.)

Order, genus	J <sub>2a</sub>	J <sub>2bj</sub>	J <sub>2bt</sub>	J <sub>2cl</sub>	J <sub>3ox</sub>	J <sub>3km</sub>	J <sub>3t(v)</sub>
<i>Belorussiella</i>							
<i>Paleogaudryina</i>							
<i>Gaudryinella</i>							
<i>Plectina</i>							
<i>Morulaplecta</i>							
<i>Karrieriella</i>							
<i>Tritaxia</i>							
<b>Order Orbitolinida</b>							
<i>Kilinanina</i>			~~~~~				
<i>Meyendorffina</i>			~~~~~				
<i>Paracoskinolina</i>		~~~~~	~~~~~				
<b>Order Involutinida</b>							
<i>Involutina</i>	~~~~~						
<i>Protopeneroplis</i>			~~~~~				-----
<i>Trocholina</i>			~~~~~				-----
<b>Order Cornuspirida</b>							
<i>Cornuspira</i>							
<i>Ophthalmidium</i>				~~~~~			-----
<i>Dolosella</i>						-----	
<i>Nubeculinella</i>							
<i>Nodobacularia</i>							
<b>Order Spirillinida</b>							
<i>Spirillina</i>			-----		~~~~~	~~~~~	-----
<i>Turrspirillina</i>							
<i>Conicospirillina</i>							
<i>Patellina</i>							
<i>Paalzowella</i>							
<i>Miliospirella</i>							
<i>Trochospirillina</i>						-----	
<b>Order Miliolida</b>							
<i>Sigmoilina</i>			-----				-----
<i>Quinqueloculina</i>			-----				-----
<i>Paleomiliolina</i>							
<i>Labalina</i>							
<i>Orthella</i>							
<i>Cornuloculina</i>							
<i>Miliolinella</i>			-----				-----
<b>Order Lagenida</b>							
<i>Lagena</i>							
<i>Ichtyolaria</i>							
<i>Geinitzinita</i>							
<i>Lingulina</i>							
<i>Nodosaria</i>							
<i>Dentalina</i>							
<i>Vaginulina</i>							

Table 1. (Contd.)

Order, genus	J <sub>2a</sub>	J <sub>2bj</sub>	J <sub>2bt</sub>	J <sub>2cl</sub>	J <sub>3ox</sub>	J <sub>3km</sub>	J <sub>3t(v)</sub>
<i>Vaginulinopsis</i>							
<i>Pseudonodosaria</i>							
<i>Lenticulina</i>							
<i>Astacolus</i>							
<i>Frondicularia</i>							
<i>Saracenaria</i>							
<i>Planularia</i>							
<i>Citharina</i>							
<i>Citharinella</i>							
<i>Marginulina</i>							
<i>Marginulinita</i>							
<i>Marginulinopsis</i>							
<i>Berthelinella</i>							
<i>Dainitella</i>							
<i>Bojarkaella</i>							
<i>Neoflabellina</i>							
<i>Falsopalmula</i>							
<i>Lingulonodosaria</i>							
<i>Spirofrondicularia</i>							
<i>Grigelis</i>							
<b>Order Polymorphinida</b>							
<i>Globulina</i>							
<i>Guttulina</i>							
<i>Eoguttulina</i>							
<i>Glandulopleurostomella</i>							
<i>Glandulina</i>							
<i>Enantiomorphina</i>							
<i>Ramulina</i>							
<i>Ramulinella</i>							
<i>Paradentalina</i>							
<i>Bullopora</i>							
<i>Pyrulina</i>							
<b>Order Rotaliida</b>							
<i>Conorboides</i>							
<i>Ceratolamarckina</i>							
<i>Cancrisiella</i>							
<i>Paulina</i>							
<i>Praelamarckina</i>							
<i>Pseudolamarckina</i>							
<i>Lamarckella</i>							
<i>Reinholdella</i>							
<i>Ceratocancris</i>							
<i>Mironovella</i>							
<i>Epistomina</i>							
<i>Epistominita</i>							
<i>Rectoepistominoides</i>							
<i>Kaptarenkoella</i>							
<i>Discorbis</i>							
<i>Ceratobulimina</i>							
<b>Order Globigerinida</b>							
<i>Eoglobigerina</i>							
<i>Globuligerina</i>							
<i>Conoglobigerina</i>							

————— - Distribution ranges of foraminifers in the Boreal and Arctic areas.

- - - - - Same in the Peritethys.

~~~~~ Same in the Tethys.

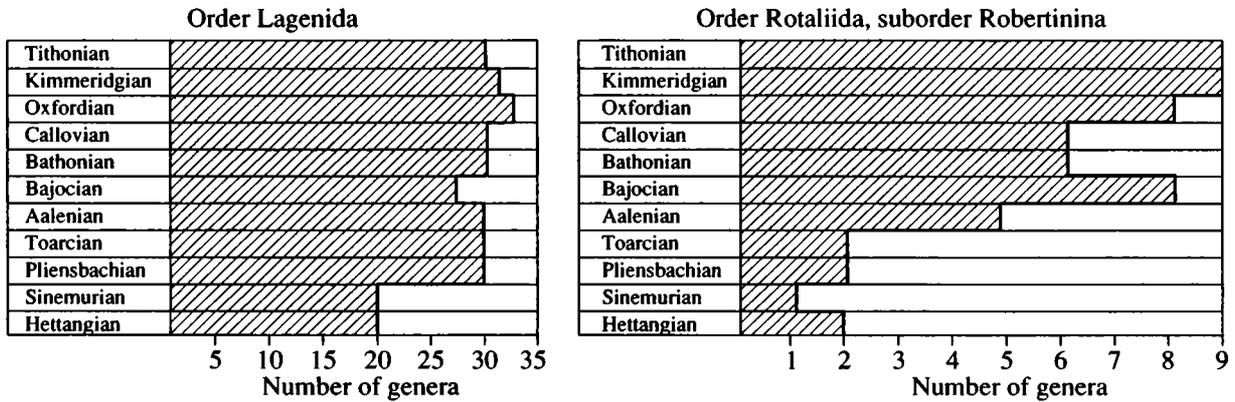


Fig. 2. Number of Jurassic genera in orders Lagenida and Rotaliida (suborder Robertinina), after Tappan and Loeblich, (1988).

Gordon (1970) was first in systematization of available data and distinguished two types of foraminiferal assemblages: shelf communities subdivided into three subtypes, and Tethyan assemblages, which include two groups. Gordon's subtypes of the shelf assemblages are as follows: (1) the nodosariid and mixed nodosariid subtype, (2) the subtype dominated by primitive agglutinated forms, and (3) the subtype of secretory benthic foraminifers different from nodosariids of the first subtype. The Tethyan foraminifers were subdivided by Gordon into assemblages with dominant agglutinated and planktonic forms.

V.A. Basov (1974) suggested the typification of foraminiferal faunas on the basis of the areal-genetic principle. He distinguished three types of fauna corresponding to various climatic zones: (1) the nodosariid-ammodiscid found in the Arctic zone; (2) the nodosariid-epistominid found in the Boreal and Subboreal moderately warm zones; and (3) the cyclaminid-pavonitid (later renamed as cyclaminid-pfenderinid) fauna of tropical and subequatorial basins characteristic of the Tethys. The typification clarified our understanding of the diversity of foraminifer assemblages and elucidated their paleobiogeographic features. Nevertheless, the subsequent accumulation of data and especially the detailed study on foraminifers from the Jurassic sections of the Tethys (northern Africa, southwestern Europe, and countries of the Eastern Mediterranean region) showed that this typification was not consistently successful as was expected. It was found that at least the cyclaminid-pfenderinid (Tethyan) and nodosariid-epistominid (Boreal) faunas inhabited the same climatic zone of the subequatorial Tethys in the Jurassic time. Geographic ranges of these dissimilar assemblages were contiguous, and changes in the composition of the assemblages occurred quickly in the lateral direction, since it was established in sections spaced only a few dozens of kilometres apart. Such abrupt changes in the composition of bottom assemblages are exemplified by the Bathonian assemblages from the Anti-Lebanon and Maritime Ranges of Syria;

the Callovian and Oxfordian assemblages from the Maritime Range of western Syria (Kuznetsova *et al.*, 1996); the Bajocian and Bathonian assemblages of Morocco (Hottinger, 1967; Sossipatrova and Rohhali, 1977); the Callovian, Oxfordian, and Kimmeridgian assemblages of Israel and Egypt (Maync, 1966; Said and Barakat, 1958); the Tithonian assemblages from the mountains and eastern area of Crimea (Gorbachik and Kuznetsova, 1994), and also from Portugal (Stam, 1986; Exton and Gradstein, 1984) and Spain (Fourcade *et al.*, 1977). Moreover, I observed in many sections that the Tethyan endemic assemblages of the cyclaminid-pfenderinid type confined to carbonate rocks alternate with assemblages of the nodosariid-epistominid type occurring in terrigenous and terrigenous-carbonate interlayers. It is notable that this alternation may have taken place within one stage or sometimes within one foraminiferal zone.

The examples cited above show that Basov's typification (1974), quite adequate as a whole, ignored an important additional factor that influenced the evolution and distribution of benthic faunas in the Jurassic seas. I believe that the bathymetric zoning of basins, important for the distribution of benthic organisms, could be such a factor. Later, Basov also demonstrated its importance for the distribution of Jurassic and Cretaceous foraminiferal assemblages, and, when analyzing their changes in various facies of the Mesozoic oceanic sediments, he showed that the composition of assemblages was dependent on the depth of their dwelling (Basov and Vasilenko, 1986; Basov, 1991).

My analysis of materials on the problem shows that the available data characterize Jurassic foraminifers from all bathymetric zones from the abyssal to littoral settings of past basins. These data are supplemented with information on the facies confinement of benthic organisms and on their taxonomic composition in all climatic zones of the Jurassic time. It should be pointed out that the climatic zones can be easily recognized by the geographic ranges of the faunas studied, whereas their bathymetric confinement is detectable on the basis

**Table 2.** Data on Jurassic deposits penetrated by deep sea drilling holes

| Region         | DSDP sites | Age of deposits (by foraminifers) | Depth (m) at present | Thickness of deposits (m) | Basin depth in the Jurassic (km) | References                          |
|----------------|------------|-----------------------------------|----------------------|---------------------------|----------------------------------|-------------------------------------|
| North Atlantic | 99         | Oxfordian–Kimmeridgian            | 4914                 |                           | Less than 3                      | Luterbacher, 1972                   |
| North Atlantic | 100        | Oxfordian–Kimmeridgian–Tithonian  | 5325                 |                           | 3                                | Luterbacher, 1972                   |
| North Atlantic | 105        | Oxfordian–Kimmeridgian–Tithonian  | 5251                 | 630                       | 3                                | Luterbacher, 1972                   |
| North Atlantic | 391C       | Tithonian                         | 4963                 | 1412                      | 3–3.5                            | Gradstein, 1978                     |
| North Atlantic | 534A       | Middle Callovian–Tithonian        | 4974                 | 1636                      | 3–3.5                            | Gradstein, 1983                     |
| North Atlantic | 367        | Oxfordian–Kimmeridgian–Tithonian  | 4758                 |                           | 3                                | Kuznetsova and Seibold, 1978        |
| North Atlantic | 416        | Tithonian                         |                      |                           | 3–3.5                            | Sliter, 1980                        |
| Indian Ocean   | 216        | Oxfordian–Kimmeridgian            | 5125                 | 542                       | 3                                | Kuznetsova, 1974; Bartenstein, 1974 |

of some features often missed by investigators, because it is difficult to recognize them in sections. As a result, we observe similar assemblages from shallow-water shelf areas of the Arctic and Boreal regions, on the one hand, and from deeper zones of tropical seas, on the other.

Naturally, other factors, such as the near-bottom temperature, the composition and character of sediments (the substrate for living organisms), the distance to the shoreline and related hydrodynamic regime, the chemistry and salinity of the water, the content of calcium carbonate in it, and the trophic and other conditions, are directly related to the bathymetric zoning of a basin.

It is difficult to present a detailed analysis of all biotic and abiotic factors in a short paper; therefore, I shall try to summarize briefly only data on principal reasons including the depth and bathymetric zones of a basin, as well as the facies type of deposits, since they all control the taxonomic composition of foraminiferal assemblages, their structure, and geographic ranges.

#### BATHYMETRIC ZONING AND COMPOSITION OF FORAMINIFERAL ASSEMBLAGES

Abyssal assemblages are established in many sections of the Jurassic deposits penetrated by deep sea drilling (Fig. 1) in the northwestern (Sites 100, 101, 105, 534) and eastern Atlantic Ocean (Sites 370, 367, 416), and also in the Indian Ocean (Sites 216, 261). Data on the Jurassic foraminifers are presented below in Table 2 modified after Gradstein (1983).

The abyssal assemblages, studied in the cited works, comprise representatives of 13 orders and about 60 genera, including forms with secretory calcite shells from the Nodosariidae, Lenticulinidae, Ceratobuliminidae, and Spirillinidae families. They indicate that sediments and coeval foraminifers were formed above the carbonate compensation depth (CCD). It is also

remarkable that Luterbacher (1972) and Gradstein (1983) reported about planktonic foraminifers of the *Globuligerina* genus in the Jurassic deposits of the abyssal bathymetric zone. The available data shows that deposits directly overlying the basaltic basement are the Late Jurassic (Oxfordian, Kimmeridgian, and Tithonian) in age. The only exception is Site 534A, where the recovered deposits are referred to the interval from the Callovian to the Tithonian (Gradstein, 1983). It should be pointed out that abyssal assemblages of foraminifers are present only in oceanic sediments penetrated by deep sea drilling. Jurassic deposits of this bathymetric zone have not been found in continents. Deposits of the bathyal zone more widespread in Jurassic sea basins are known in a section of the northwestern Atlantic Ocean (the Bahamas region), western Europe (Holzer, 1969; Feninger and Holzer, 1970), and Arctic Canada (Hedinger, 1993).

Along with primitive agglutinated forms from the Astorhizida order, the bathyal foraminiferal assemblages comprise ammodiscids, litiolids, and trochamminids. Foraminifers with a secretory shell (lagenids and epistominids) are less abundant. Planktonic foraminifers have not been found. Hedinger (1993) reported on the characteristic composition of foraminiferal assemblages from the Upper Jurassic deposits (the Oxfordian–Volgian) studied in the Richardson Mountains (the Aklavik Range of Arctic Canada). The assemblage from clay and shale beds of the Husky Formation includes here 95 species of agglutinated foraminifers belonging to 29 genera, as well as 46 secretory species of 20 genera. The density of these populations is as high as more than 100 shells per g of the rock sample.

The foraminiferal assemblages from the Middle Jurassic sections of the Central Atlas (Morocco) presumably characterized the bathyal and partly epibathyal deposits (Sossipatrova and Rohhali, 1977) (Fig. 1). Lagenids comprising the diverse and abundant *Citharina*, *Lenticulina*, *Astacolus*, and *Planularia* species are

the dominant group. Similar but more diverse assemblages, which include litoiids, trochamminids, and ataxophragmiids, are described from the Middle Jurassic (Aalenian–Callovian) deposits of France (Wernli, 1971), the Middle and Upper Jurassic deposits of Germany (Lutze, 1960), and from the eastern Atlantic Ocean (Riegraf *et al.*, 1984; Sliter, 1980).

The transition to the epibathyal zone is marked by an enrichment and transformation of foraminiferal assemblages, in which epistominids and ceratobuliminids (the Rotaliida order), coexisting with diverse agglutinated and secretory foraminifers, play a leading role (Fig. 1). The geographic range of these assemblages is wider than that of the bathyal assemblages. They are known from the Middle and Upper Jurassic (Callovian–Tithonian) deposits of Portugal (Stam, 1986), the Oxfordian deposits of France (Bastien and Sigal, 1962), and the Middle and Upper Jurassic (Bathonian–Tithonian) deposits of Madagascar (Espitalié et Sigal, 1963), southern England (Cordey, 1963; Lloyd, 1959, 1962), central Poland (Bielecka, 1960; Bielecka and Styk, 1981), eastern Crimea (Kuznetsova and Gorbachik, 1985), Sinai (Said and Barakat, 1958), and the Anti-Lebanon Ridge in Syria (Kuznetsova, 1994; Kuznetsova and Dobrova, 1995; Kuznetsova *et al.*, 1996). The presence of *Globuligerina bathoniana* (Pazdro), *G. oxfordiana* (Grig.), and *G. calloviensis* Kuzn. is characteristic of sections in Syria, Crimea, Poland, and Portugal.

The further taxonomic diversification of foraminiferal assemblages is observed in the transition to the shallower areas of sea basins representing their sublittoral zone. The geographic differentiation of benthic assemblages from this zone becomes more pronounced. However, nodosariids (diverse ornamented and psilate *Lenticulina*, *Marginulina*, *Marginulinopsis*, *Citharina*, and *Citharinella* genera) and diverse genera and species of epistominids are still the dominant groups. Forms with agglutinated shells such as large *Ammobaculites*, *Haplophragmoides*, *Evolitinella*, *Kutsevella* and other genera of litoiids preserve their significance. Abundant polymorphinids inhabited areas remote from the shoreline, where the hydrodynamic regime was less active. Benthic foraminifers of the sublittoral zone are clearly differentiated in accordance with latitudinal and climatic zones. In the Boreal areas, they are diverse and have the above-mentioned taxonomic composition, but, despite a good preservation, they rarely occur in abundance. The sublittoral and littoral deposits are known on the Russian platform, where in the lectostratotype of the Volgian Stage there is the bathymetric succession of the bathyal (?) (the upper Kimmeridgian–lower Volgian), epibathyal (the middle Volgian), and sublittoral to littoral (the upper Volgian) sediments. The deposits of the littoral zone are represented by shallow-water sediments, namely, by quartz, glauconite, and polymictic sands and sandstones, in places coarse-grained, which show numerous traces of erosional unconformities. These sediments

bear a peculiar foraminiferal assemblage exclusively consisting of nodosariids, mainly of *Marginulina* species (Kuznetsova, 1979, Fig. 22).

Foraminiferal assemblages quite different in taxonomic composition inhabited shallow-water marine sediments of the Tethys. Cyclaminid–pfenderinid assemblages populated shallow and warm zones of sea basins rich in calcium carbonate. Such assemblages of larger foraminifers are unknown beyond the limits of these bathymetric zones of the Tethys. The assemblages include genera *Paleopfenderina*, *Meyendorffina*, *Kilianina*, *Timidonella*, *Alzonella*, *Paracoskinolina*, *Dhrumella*, *Paraurgonina*, *Haurania*, *Kurnubia*, *Redmondoides*, *Riyadhella*, *Bramkampella* and others. Representatives of nodosariids, epistominids, polymorphinids, and other smaller foraminifers either are not present or are represented by single shells seldomly encountered. Many genera and families of these assemblages are endemic. The species diversity is very low, whereas the density of populations for some species is very high (up to 1000 specimens per 100 g of dry rock). This is especially typical of genera *Kurnubia*, *Pseudocyclamina*, *Choffatella*, and *Anchispirocyclus*. Assemblages of this composition are present in the Bathonian, Callovian, Oxfordian (very locally), Kimmeridgian, and Tithonian deposits of Syria (Kuznetsova *et al.*, 1996), France (Peybernes, 1976), the eastern Carpathians (Dragastan, 1975), Sardinia (Azema *et al.*, 1977), Antalia (Bassoulet and Poisson, 1975), and Morocco (Hottinger, 1967). Incomplete assemblages consisting of *Anchispirocyclus*, *Choffatella*, and *Bramkampella* forms are found in the Tithonian carbonate rocks of the Crimea Mountains (Gorbachik and Kuznetsova, 1994) (Fig. 1). A brief review of the taxonomic composition of foraminiferal assemblages and their distribution in bathymetric zones of the Jurassic sea basins shows that the Jurassic benthic assemblages inhabited the whole series of settings from the abyssal to the littoral zones. Geographic ranges of Jurassic abyssal assemblages were limited.

More diverse assemblages, which include more than 60 genera of agglutinated and secretory foraminifers, are present in sediments from the depth of 2000–3500 m and have wider geographic ranges (the northwestern and central Atlantic and Indian Ocean). They are known only in oceanic sections, where the Upper Jurassic sediments directly overlie the basaltic basement.

The bathyal zone shows again the increasing taxonomic diversity of foraminiferal assemblages comprising here more than 80 genera with secretory and agglutinated shells, and also planktonic foraminifers appeared for the first time. The geographic range of assemblages from this zone is also widened, and they are known in northern, western, and central Europe; in the northern Russian platform; northern Siberia; Arctic islands; northwestern Africa; Hindustan; and the eastern Atlantic Ocean. The geographic differentiation of their taxonomic composition is poorly pronounced.

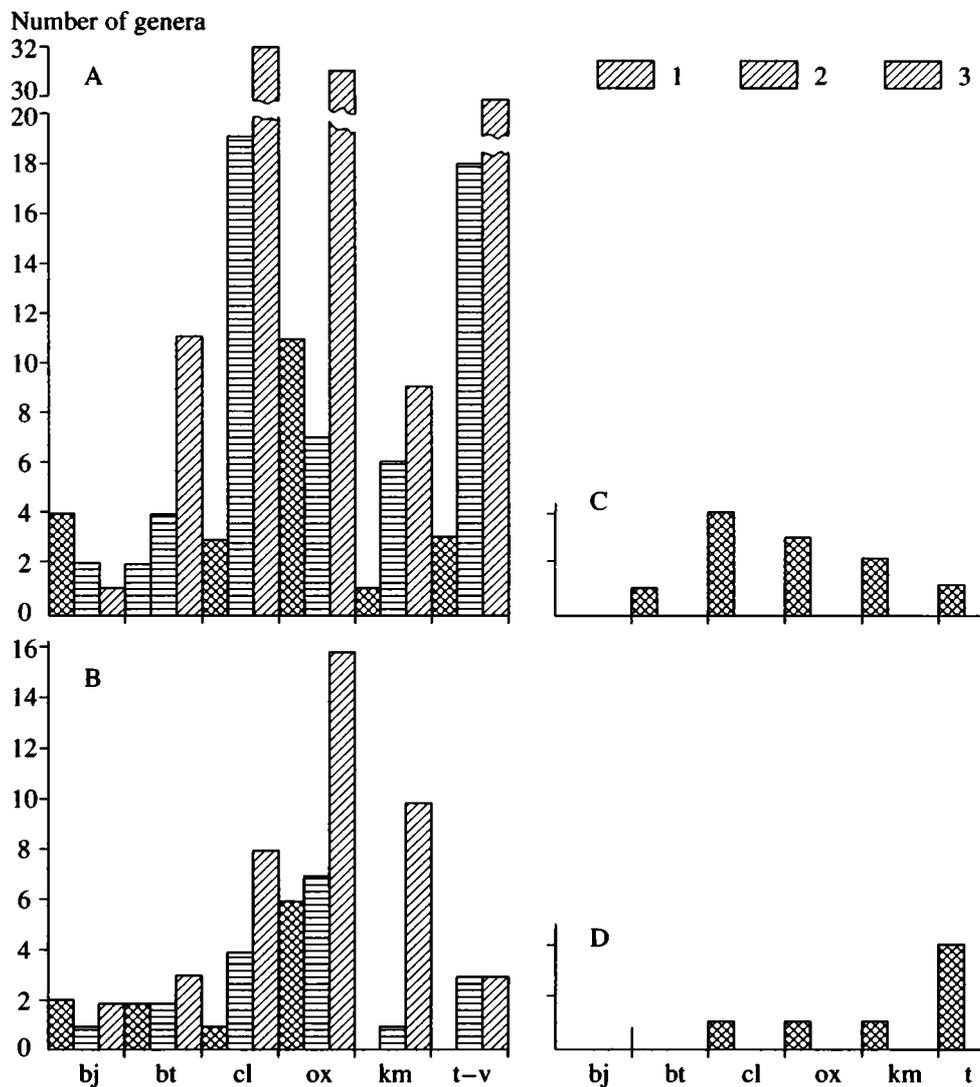


Fig. 3. Dynamics of species diversity in dominant genera of the Boreal and Tethyan fauna types of foraminifers: (1) Syria; (2) Crimea; (3) Russian platform and England. (A) *Lenticulina* and (B) *Epistomina* genera of the nodosariid-epistominid fauna type. (C) *Kur-nubia* and (D) *Pseudocyclammina* genera of the cyclaminid-pfenderinid fauna type.

The epibathyal and outer sublittoral zones (500–200 m deep) display the presence of abundant and diverse foraminiferal assemblages, which inhabited wide areas in the Boreal and Tethyan provinces during the Jurassic. The number of genera, which belong to 16 orders, increases up to 100–110. The geographic differentiation is distinct.

The middle and inner sublittoral (200–100 m deep) and littoral zones comprise foraminiferal assemblages diverse in composition and including more than 100 genera. The geographic and climatic differentiation is extremely high. The number of endemic genera and families increases in the Tethys, whereas the diversity of endemic species grows in the Boreal zone. Geographic ranges of these assemblages are limited.

Changes in the taxonomic composition of foraminiferal assemblages in different bathymetric zones of the Jurassic seas show that, in addition to the long-lived cosmopolitan genera demonstrating a high degree of tolerance and wide geographic ranges, the assemblages in question also comprise endemic genera of highly specialized forms with a lower degree of tolerance, more limited geographic ranges, and, as a rule, shorter existence periods. Other peculiar features of genera of the two aforementioned types—endemic and cosmopolitan—are interesting as well. The quantitative analysis of generic and specific diversity is important, first of all for those genera that dominate in the different-type assemblages, i.e., in the Boreal nodosariid-epistominid (widespread) and Tethyan cyclaminid-pfenderinid (endemic) faunas (Fig. 3).

When the number of species of each indicated genera is compared, a clear regularity becomes obvious. The *Lenticulina* genus is present in deposits of all stages in territories under comparison, although the number of species of the genus in Syria, the Crimea, and the Russian platform differs greatly (Fig. 3A). For instance, the number of *Lenticulina* species in the Bathonian deposits is 2 in Syria, 4 in the Crimea, and 11 in the Russian platform. The distinction is even sharper for the Callovian and Oxfordian deposits. The Callovian deposits of the *Lenticulina* genus comprise 3 species in Syria, 19 in the Crimea, and 32 in the Russian platform. The Oxfordian deposits of Syria are known to include 11 species of the *Lenticulina* genus, while 7 are reported from the Crimea and 31 from the Russian platform. Some decrease in the species diversity of the *Lenticulina* genus is observed in the Kimmeridgian, but, in the Tithonian (Volgian), the number of species of the genus increases abruptly: the deposits of this age in the Crimea and Russian platform comprise 18 and 30 species, respectively, and they yielded only 4 species in Syria. A similar distribution trend is characteristic of *Epistomina* species, the second group dominant in the assemblages under consideration (Fig. 3B).

In other words, when cosmopolitan genera prevail in the Jurassic assemblages, the species diversity in the Jurassic basins of Syria is less than that in the Peritethyan basins of the same age and, especially, in the Russian platform and England, where these forms, diverse and abundant, are most widespread and dominant. Cosmopolitan genera, which have the widest (subglobal) geographic ranges, have long been existing, and many of them are known from the Early Mesozoic to the present day. A high species diversity is another characteristic feature of these fauna types that distinguishes them from the Tethyan endemic genera. The latter, exhibiting a low tolerance, high specialization, intricate shell structure, and limited geographic ranges, have narrow stratigraphic ranges and a low species diversity. Among 22 endemic genera that lived in the Jurassic tropical seas, more than half of them are represented by one species (genera *Dhrumella*, *Haurania*, *Amijiella*, *Meyendorffina*, *Timidonella*, *Alzonella*, *Flabellacyclolina*, and *Paracoskinolina*) or by 2 to 3 species (genera *Pseudocyclamina* and *Paleopfenderina*), and only some of them (*Kurnubia*, *Redmondoides*, and *Riyadhella*) are more diverse in species composition (Fig. 3C, 3D).

Hence, the analysis of the generic composition of the Jurassic foraminiferal assemblages and dynamics of their species diversity showed that nodosariids and epistominids had the highest species diversity and highest degree of tolerance among other benthic foraminifers in the Jurassic period of their evolution. Many genera of these families comprise species with narrow stratigraphic ranges, which is very important for the detailed subdivision of the Jurassic sediments and their correlation. The species diversity of endemic genera (Tethyan and Boreal endemics) was considerably

lower, and their life period was limited, not exceeding, as a rule, a stage, i.e., a geological age.

The analysis of taxonomic composition of foraminiferal assemblages from different climatic and bathymetric zones allows me to conclude that changes related to the bathymetric zoning are similar to those that are dependent on the geographic (climatic) position of the assemblages in the Jurassic sedimentary basins. The only exception is the foraminiferal community of the tropical littoral and sublittoral zones, which is unique, as compared to assemblages from other bathymetric and climatic zones of the Jurassic sea basins.

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