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Benthic foraminiferal turnover and the paleoenvironmental evolution of the Maikop Basin: From agglutinated to calcareous dominance (Kerch Peninsula, late Oligocene–Middle Miocene)

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Abstract: Based on the revision of archival data by M.F. Kozyreva (1947–1949) and their modern reinterpretation, the paleoecological evolution of the Maikop Basin on the Kerch Peninsula sector during the Late Kerleutian–Tarkhanian (late Oligocene–Middle Miocene) was reconstructed using benthic foraminifera. Presence/absence data were analysed using Jaccard cluster analysis, taxa richness (S), and morphogroup analysis of agglutinated taxa, which allowed for the reconstruction of the temporal evolution of benthic foraminiferal assemblages, associated bottom-water environmental changes, and four successive phases of ecosystem transformation at local and basin-wide scales. The initial phase (Late Kerleutian–early Sakaraulian) was characterised by persistent agglutinated assemblages under relatively stable bathyal conditions, with recurrent *Bathysiphon* crises associated with reduced bottom-water circulation. The late Sakaraulian records the first calcareous inversion and local ecological restructuring within the existing bathyal basin. The Kotsakhurian records the regional ecological crisis, which is expressed by the widespread occurrence of monospecific *Saccammina zuramakensis* assemblages under hydrochemical instability. The Tarkhanian records a second calcareous inversion that is fundamentally different from the Sakaraulian event. It reflects basin shallowing toward outer sublittoral settings, increased marine connectivity, faunal renewal, and improved bottom-water oxygenation, while the characteristic Maikop-type of sedimentation was still maintained. These results demonstrate that, during the Late Kerleutian–Tarkhanian evolution of the Maikop Basin on the Kerch Peninsula sector, both local and regional environmental reorganisations elicited a recurrent pattern of benthic assemblage response, which is characterised by ecological crises followed by renewal.

Keywords: benthic foraminifera, Maikop Basin, Eastern Paratethys, paleoenvironmental evolution, taxonomic inversion, late Oligocene–Middle Miocene, Kerch Peninsula

Introduction

Deposits in the Maikop Basin have long been studied primarily for stratigraphic purposes. On the Kerch Peninsula (Fig. 1), these deposits were studied in detail during a large-scale geological survey in the 1950s. A significant contribution to their study was made by M.F. Kozyreva, a paleontologist at the Krymneftegeologiya Trust, who studied the foraminifera of the Maikop Group on the Kerch Peninsula (based on Kozyreva's geological reports from 1947 to 1949; summarised and interpreted in Vernyhorova & Ryabokon 2018). Her work served as the stratigraphy basis for the late Oligocene–Early Miocene deposits in the Eastern Paratethys (e.g., Maimin 1951; Muratov 1969; Teslenko 1984). The identified stratigraphic horizons remain the primary criteria for the stratigraphic division of Oligocene–Lower Miocene deposits (Kerleutian, Caucasian, Sakaraulian, and Kotsakhurian regional stages) in Southern Ukraine to this day. However, evolution of benthic foraminiferal assemblages and the paleoecological evolution of the Maikop Basin during this time interval have remained insufficiently understood.

In previous studies (Vernyhorova 2014, 2015, 2016; Vernyhorova & Ryabokon 2018, 2020), a detailed lithological and paleontological analysis of these deposits was carried out, and the regional stratigraphic scheme was clarified. Particular attention was paid to the sections of the Kerch Peninsula, since one of the most complete stratigraphic records in Southern Ukraine can be traced there. Further analysis of Kozyreva's archival reports (1947–1949), along with their modern reinterpretation, revealed a clear, but previously unrecognised pattern in the succession of benthic foraminiferal assemblages during the Late Kerleutian–Kotsakhurian. A detailed biostratigraphic and paleoecological analysis of the Tarkhanian benthic foraminiferal assemblages was performed (Vernyhorova et al. 2023).

This study aims to reconstruct the paleoecological evolution of the Maikop Basin in the Kerch Peninsula sector through

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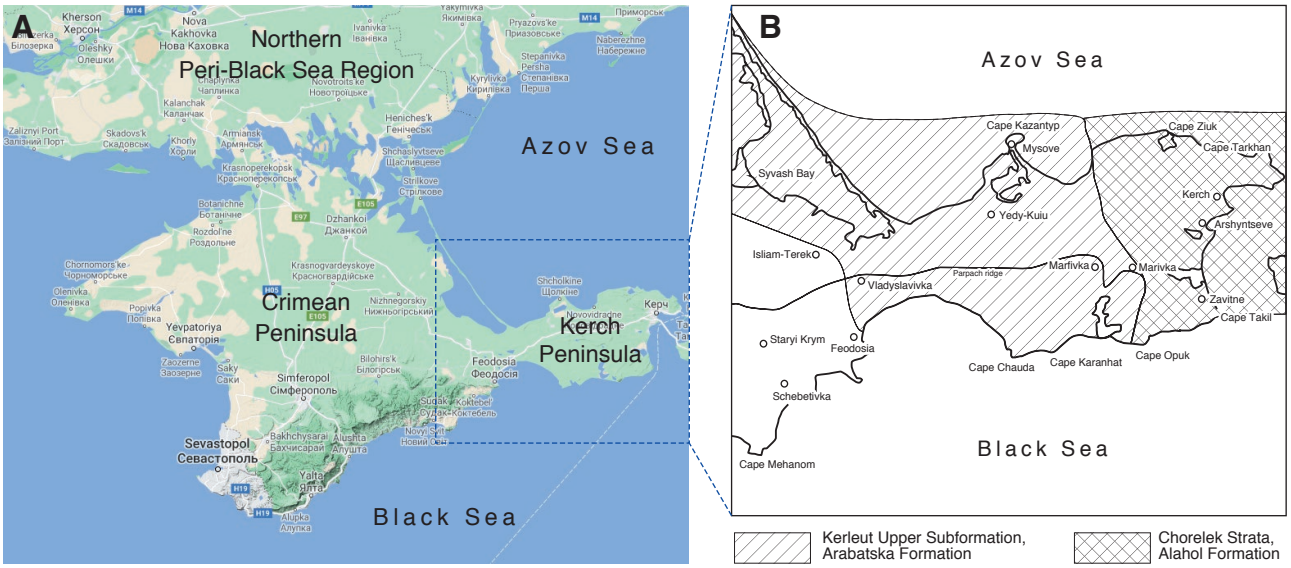


Fig. 1. Geographic setting of the Kerch Peninsula and distribution of the stratigraphic units discussed in this study. **(A)** Geographic location of the Kerch Peninsula (Google Maps). **(B)** Distribution of the Arabatska Formation within the Central and North Kerch structural-facies subzones and the Alahol Formation within the East Kerch structural-facies subzone. Within the Kerch Peninsula, their distribution coincides with that of the Upper Kerleut Subformation and Chorelek Strata, respectively (after Vernyhorova & Ryabokon 2018, 2020).

an integrated analysis of benthic foraminiferal assemblages spanning the Late Kerleutian–Tarkhanian. In order to achieve this, the composition and ecological structure of foraminiferal assemblages were analysed, quantitative analyses were performed, and the major phases of benthic ecosystem reorganisation were identified and interpreted in terms of basin evolution.

Materials and methods

Archival materials

The present study is based on published and archival data on benthic foraminifera from the Maikop deposits of the Kerch Peninsula. Particularly important are the results of detailed micropaleontological investigations conducted by M.F. Kozyreva in the period 1947–1949 during geological mapping of the Kerch Peninsula. These materials include taxa lists from individual core intervals along with their stratigraphic interpretations. The following geological reports by M.F. Kozyreva were analysed (covering material from approximately 7000 core samples):

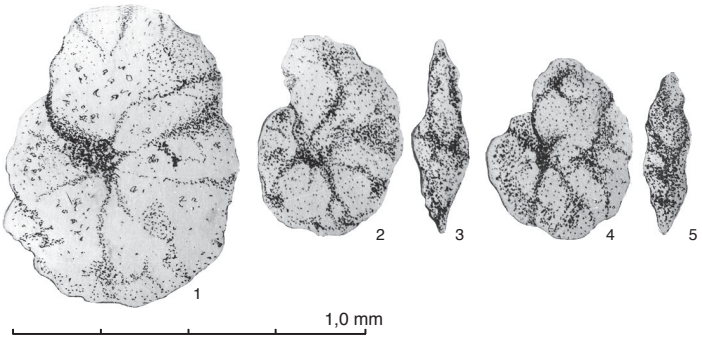
- Study of the microfauna of the Maikop deposits of Crimea (Kerch Peninsula). *Krymneftegeologiya Trust*, Feodosiya. 1947, 31 p.
- Report on the study of the microfauna of the Oligocene and Miocene deposits of Crimea. *Krymneftegeologiya Trust*, Feodosiya. 1948, 202 p.
- Generalisation of data on the stratigraphy of the Maikop deposits of Crimea based on microfauna. *Krymneftegeologiya Trust*, Feodosiya. 1949, 330 p.

These archival reports provide species occurrence data for benthic foraminifera along with the original stratigraphic interpretations and qualitative descriptions of the assemblages. They also serve as an additional source for interpreting the statistical patterns and paleoenvironmental trends identified in the present study.

The primary data were critically reviewed and systematised in accordance with modern concepts of benthic foraminiferal taxonomy and ecology. Taxonomic names follow current nomenclature. In cases where the modern taxonomic interpretation of a species or genus is uncertain or ambiguous, the original name is retained in the text, while an asterisk is added to the Figures (e.g., **Haplophragmoides kerleuticus* Kozyreva; **Pulvinulinella*). The complete set of paleontological plates from Kozyreva's reports (1947–1949) was previously published in Vernyhorova & Ryabokon (2018). The present study reproduces selected illustrations of benthic foraminiferal taxa from these plates.

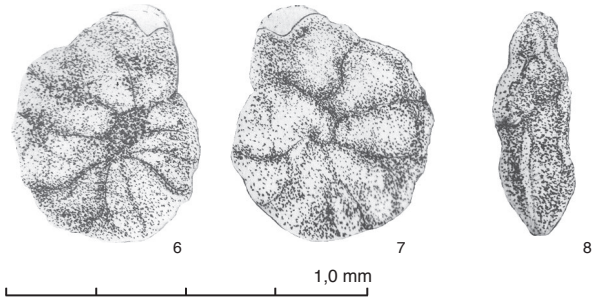
To reconstruct the original taxonomic concept of the unpublished index species of the Upper Kerleut Subformation, *Haplophragmoides kerleuticus* Kozyreva (manuscript name), all available information from Kozyreva's archival reports (1947–1949) (including original illustrations, morphological observations, and stratigraphic distribution) was critically compiled and summarised (Fig. 2). Kozyreva reported transitional forms between *H. kerleuticus* and *H. periferoexcavata* Subbotina, 1936. Therefore, the original published illustration of *H. periferoexcavata* (Ryabinin & Korobkov, 1949) is included for comparison. The original illustration of *H. kjurendagensis* Morozova, 1949 is reproduced because this species was subsequently mentioned in the literature in connection with *H. kerleuticus*; however, without taxonomic justification.

Reconstruction of the original concept of *Haplophragmoides kerleuticus* Kozyreva, manuscript name
(based on the original unpublished materials of Kozyreva, 1947-1949)



Haplophragmoides kerleuticus Kozyreva, manuscript name
(unpublished geological reports by Kozyreva, 1947-1949)

Test dimensions (mm):
1: maximum diameter – 1.13; minimum diameter – 0.75; thickness – 0.11.
2, 3: maximum diameter – 0.53; minimum diameter – 0.37; thickness – 0.11.
4, 5: maximum diameter – 0.45; minimum diameter – 0.37; thickness – 0.11.
Kerch Peninsula, Middle Maikop, Upper Kerleutian.



Haplophragmoides periferoexavata Subbotina
(unpublished geological reports by Kozyreva, 1947-1949)

Test dimensions (mm):
6, 7, 8: maximum diameter – 0.60; minimum diameter – 0.45.
Kerch Peninsula, Upper Maikop, *Bathysiphon* Horizon.

1. Taxonomic status.
– Described by Kozyreva as a new species (*H. kerleuticus* sp. nov.), clearly distinguished from other representatives of the genus *Haplophragmoides*.

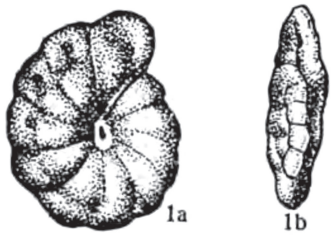
2. Reported diagnostic characters.
– Morphology: relatively large, flattened tests with a very thin, often translucent peripheral margin and numerous chambers arranged in two whorls. The test wall is composed of fine agglutinated material.
– Variability: smaller specimens of *H. kerleuticus* occur in some beds, particularly in the upper part of the Upper Kerleutian.
– Transitional forms: transitional specimens between *H. kerleuticus* and *H. periferoexcavata* were reported from the Mamat area of the Kerch Peninsula.

3. Stratigraphic significance.
– Index taxon of the Upper Kerleutian, occurring abundantly throughout the Middle Maikop deposits of the Kerch Peninsula.
– Beds characterized by *H. kerleuticus* were defined as the first microfaunal reference horizon within the Maikop succession and regarded as an important regional marker; commercial oil inflows were associated with this interval.
– The first appearance of *H. kerleuticus* was considered to mark the upper boundary of the Middle Oligocene.

4. Distribution outside the Kerch Peninsula.
– according to the published and unpublished data available at that time, no comparable assemblages had been reported from the Maikop deposits of the Kuban region or the North Caucasus.

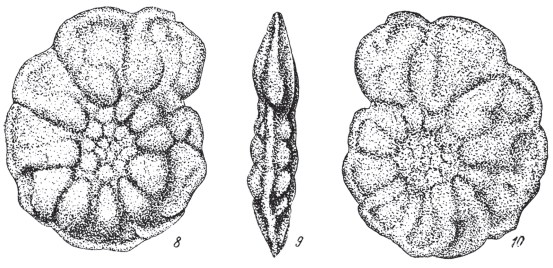
Subsequent usage of the species name in the literature.
1947-1949 – *Haplophragmoides kerleuticus* sp. nov. (unpublished geological reports by Kozyreva).
1958 – cited as *Haplophragmoides kjurendagensis* Mor. (*H. kerleuticus* sp.) (Golubnichaya in Dikenshtein 1958; Syabray 1963); no explanation for the taxonomic reinterpretation was provided.
1969 – cited as *Haplophragmoides kjurendagensis kerleuticus* Kozir. (Muratov 1969); no explanation for the taxonomic reinterpretation was provided.
2018 – the original name *Haplophragmoides kerleuticus* was restored during the revision of Kozyreva's archival materials (Vernyhorova & Ryabokon 2018).

Taxa cited in the taxonomic history of *H. kerleuticus*



Haplophragmoides periferoexcavata Subbotina, 1936
(Subbotina 1936; reproduced from Ryabinin & Korobkov 1949)

Test dimensions (mm): diameter of the largest specimens – 0.9; diameter of the smallest specimens – 0.5.
1a – lateral view; 1b – peripheral view.
North Caucasus, Maikop deposits, Olginska Formation.



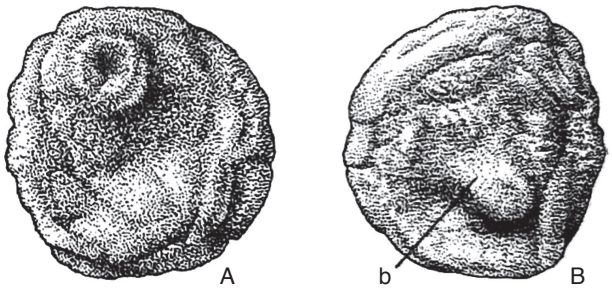
Haplophragmoides kjurendagensis Morozova, 1949
(Morozova 1949; original illustration)

Test dimensions (mm): test diameter – 0.72; thickness – 0.12.
Southern Turkmenia, Lower Oligocene.

Fig. 2. Reconstruction of the original taxonomic concept and subsequent taxonomic history of *Haplophragmoides kerleuticus* Kozyreva (manuscript name), based on Kozyreva's unpublished archival materials (1947–1949; the complete set of plates was previously published in Vernyhorova & Ryabokon 2018). Original unpublished illustrations and diagnostic characteristics of *H. kerleuticus* are compared with the original published illustrations of *H. periferoexcavata* Subbotina, 1936 (reproduced from Ryabinin & Korobkov 1949) and *H. kjurendagensis* Morozova, 1949 (reproduced from Morozova 1949), along with a summary of the subsequent usage of the name in the literature.

Figure 2 also summarises the subsequent use and taxonomic interpretation of the name *H. kerleuticus* in the literature.

The original published illustration of *Saccammina zuramakensis* Bogdanovich, 1954 (see Bogdanovich 1954) is included here as the zonal index species of the Kotsakhurian Regional Stage (Fig. 3).



Saccammina zuramakensis Bogdanovich, 1954
(Bogdanovich 1954; original illustration)

Test dimensions (mm): 0.35-0.60
Wall thickness (cross section, mm): 0.025-0.040
A – top view, B – bottom view, b – tubercle
Southern Dagestan, Ullu-Chay River.

Fig. 3. Original published illustration of *Saccammina zuramakensis* Bogdanovich, 1954, the index species of the Kotsakhurian Regional Stage, reproduced from the original description (Bogdanovich 1954).

Regional stratigraphic framework and terminology

Regional stratigraphic terminology follows the Stratigraphic Code of Ukraine (Gozhyk 2012) and the framework traditionally used for the Eastern Paratethys (Zhamoida 1977, 1988). In addition to regional stages and substages, this framework recognises regional horizons.

Regional horizons are regionally traceable stratigraphic intervals distinguished within a Regional Stage or Substage by one or more characteristic features that permit reliable regional correlation. In the Eastern Paratethys, these features often include specific fossil assemblages, the dominance of particular taxa, or a combination of paleontological and lithological criteria. Regional horizons are widely used as mapping units in regional geological mapping and stratigraphic correlation.

Unlike formal biozones defined in the International Stratigraphic Guide (https://stratigraphy.org/guide/), regional horizons are elements of the regional stratigraphic framework rather than biostratigraphic units.

The *Bathysiphon* Horizon was originally proposed by M.F. Kozyreva as a regional marker for the subdivision and correlation of the Upper Maikop succession on the Kerch Peninsula, based on the characteristic occurrence of *Bathysiphon*. This regional stratigraphic unit was subsequently incorporated into the regional stratigraphic scheme of Southern Ukraine (Teslenko 1984).

Data analysis

The compiled dataset has been used in previous studies to support the stratigraphic framework of the Upper Kerleutian –Tarkhanian (upper Oligocene–Middle Miocene) deposits of Southern Ukraine (Vernyhorova & Ryabokon 2018, 2020; Vernyhorova et al. 2023). Here, it is employed as the basis for quantitative and paleoecological analyses.

The statistical analyses were performed using presence/absence (binary) data. In order to characterise the taxonomic structure of benthic foraminiferal assemblages, the proportions of identified taxa were calculated. The reported percentages (e.g., agglutinated versus calcareous taxa or ecological groups) represent the relative contribution of taxa to the total species richness within each stratigraphic interval rather than specimen abundance or population density. Consequently, the statistical analyses characterise broad temporal changes in assemblage composition and ecological structure rather than changes in the number of individuals. The analyses were performed at the level of benthic foraminiferal assemblages defined for individual stratigraphic intervals, each of which was treated as an independent taxonomic unit for subsequent statistical and paleoecological comparison.

The possible effects of differential preservation between agglutinated and calcareous foraminiferal tests were considered during paleoecological interpretation. The studied succession consists predominantly of lithologically-uniform Maikop clays, with no significant changes in depositional facies throughout the studied succession. Although differential preservation between agglutinated and calcareous tests cannot be completely excluded (e.g., Murray 2006), the recurrent alternation of agglutinated- and calcareous-dominated assemblages within this lithologically-uniform succession suggests that the observed taxonomic patterns primarily reflect ecological changes rather than selective dissolution or differential preservation of tests.

Statistical calculations were carried out using the PAST software package (Hammer et al. 2001; version 4). Benthic foraminiferal data were organised as a binary presence/absence matrix. The following analyses were performed: taxonomic similarity of assemblages using the Jaccard similarity coefficient and UPGMA clustering algorithm, taxonomic richness (Taxa_S index), pairwise similarity between assemblages, and morphogroup structure of agglutinated taxa.

Taxonomic similarity of assemblages

Cluster analysis was performed using the Jaccard similarity coefficient and the paired-group (UPGMA) clustering algorithm. In order to evaluate taxonomic similarity independent of geological time, similarity dendrograms without stratigraphic constraints were constructed. Additionally, in order to compare taxonomic similarity with the observed stratigraphic succession, a similarity dendrogram was generated using the stratigraphic constraint option.

Taxonomic richness and taxonomic proportions

Taxonomic richness (Taxa_S) was calculated for each assemblage. The proportions of agglutinated versus calcareous taxa were expressed as percentages of the total taxa richness within each benthic foraminiferal assemblage and regarded as presence/absence-based measures.

Pairwise taxonomic similarity (Similarity matrix)

Pairwise taxonomic similarity among assemblages was calculated using the Jaccard similarity coefficient based on the same presence/absence matrix. The resulting similarity matrix was displayed as a heatmap to visualise the degree of taxonomic similarity between assemblages.

Morphogroup analysis of agglutinated taxa

Agglutinated taxa were assigned to functional morphogroups following Kaminski & Gradstein (2005). The generalised ecological characteristics summarised below are based primarily on this classification and are used as generalised ecological descriptors, since individual taxa may display considerable ecological plasticity.

Stratigraphy of the Maikop deposits of the Kerch Peninsula sector (upper Oligocene–Middle Miocene)

In the Eastern Paratethys, especially in Southern Ukraine, the Maikop Basin existed from the Oligocene to the early Middle Miocene, within which a thick clayey succession of the Maikop Group accumulated. In classical stratigraphic schemes, its stratigraphic extent is limited to the Kotsakhurian time (e.g., Borissjak 1937), whereas the Tarkhanian deposits were treated as a new, independent stage of basin development separate from the Maikop succession. Following Andrusov (1889, 1918), the Tarkhanian deposits are considered here as the final stage of the Maikop Basin evolution and the upper part of the Maikop succession, which serves as the basis for the current research (see also Vernyhorova et al. 2023).

The studied section of the Kerch Peninsula comprises deposits of the Middle Subgroup (Upper Kerleutian) and the Upper Subgroup (Caucasian–Tarkhanian) of the Maikop Group, which was previously characterised by specific marine environmental conditions that strongly influenced biotic evolution (Andrusov 1918; Borissjak 1937; Maimin 1951; Muratov 1969; Teslenko 1984; Nosovsky 1993; Barg & Stepanyak 2003; Vernyhorova 2014; Vernyhorova & Ryabokon 2018, 2020).

In the regional stratigraphic framework of the Eastern Paratethys, the studied succession includes deposits of three formations of the Maikop Group that correspond to the upper part of the Kerleutian (upper Oligocene), as well as the Caucasian, Sakaraulian, Kotsakhurian (Lower Miocene), and Tarkhanian (Middle Miocene) regional stages (Fig. 4). Their detailed lithological and paleontological description, discussion of their stratigraphic position, and a comprehensive reference list are available elsewhere (Vernyhorova & Ryabokon 2018, 2020; Vernyhorova et al. 2023).

Within the studied section, the following lithostratigraphic units are recognised (Fig. 4):

- Upper Subformation of the Kerleut Formation (Upper Kerleutian, upper Oligocene). It is widespread in the western and central parts of the Kerch Peninsula. It is represented by grey, dark grey, and olive-grey non-carbonate clays with a brownish tint, silty or slightly sandy, with millimeter-scale interbeds of lighter siltstone and fine-grained sand, as well as layers and concretions of yellowish-brown siderite; the thickness is 450–650 m; a high sand content and an alternating pattern of sandy and clayey layers are characteristic features of these deposits (e.g., Maimin 1951; Vernyhorova & Ryabokon 2018, 2020).
- Arabatska Formation (Caucasian, Sakaraulian, Kotsakhurian, and Tarkhanian regional stages). It is widespread in the western and central parts of the Kerch Peninsula. It consists of relatively uniform dark grey, olive-brown, and grey-brown clays, often with sand admixtures and inclusions, slightly sandy; the thickness reaches up to 1200 m; sandy grains on the bedding planes and thin interbeds of clay siderites are characteristic features of these deposits (e.g., Maimin 1951; Barg & Stepanyak 2003; Vernyhorova 2014).
- Alahol Formation (Caucasian, Sakaraulian, Kotsakhurian, and Tarkhanian regional stages). It is distributed in the western and central parts of the Kerch Peninsula and is laterally equivalent to the Arabatska Formation. It is represented by grey, dark grey to black, brownish-grey, and olive-grey non-carbonate clays, laminated, detrital, and slightly sandy; numerous siderite concretions are characteristic, occasionally accompanied by crystalline gypsum and jarosite coatings; thickness is up to 700 m; the main lithological distinction from the Arabatska Formation is the absence of siderite layers and the predominance of siderite concretions (Vernyhorova 2014; Vernyhorova et al. 2023).

The stratigraphic subdivision of the Maikop deposits of the Kerch Peninsula is based on changes in benthic foraminiferal assemblages. These characteristic assemblages were originally recognised based on their distinctive taxonomic composition and provide the basis for regional stratigraphic correlation (based on Kozyreva's reports, 1947–1949; summarised and interpreted in Vernyhorova & Ryabokon 2018). The following characteristics summarise the criteria used to distinguish these assemblages, based on Kozyreva's archival reports and subsequent published sources:

- *Haplophragmoides kerleuticus* assemblage: upper part of the Upper subformation of the Kerleut Formation (Upper Kerleutian), stratigraphic thickness 450–650 m; characterised by an assemblage composed almost exclusively of agglutinated taxa, with *H. kerleuticus* found in large numbers of tests (after Kozyreva's reports, 1949).
- *Haplophragmoides periferoexcavata* assemblage: Arabatska Formation (Caucasian), stratigraphic thickness 450–500 m;

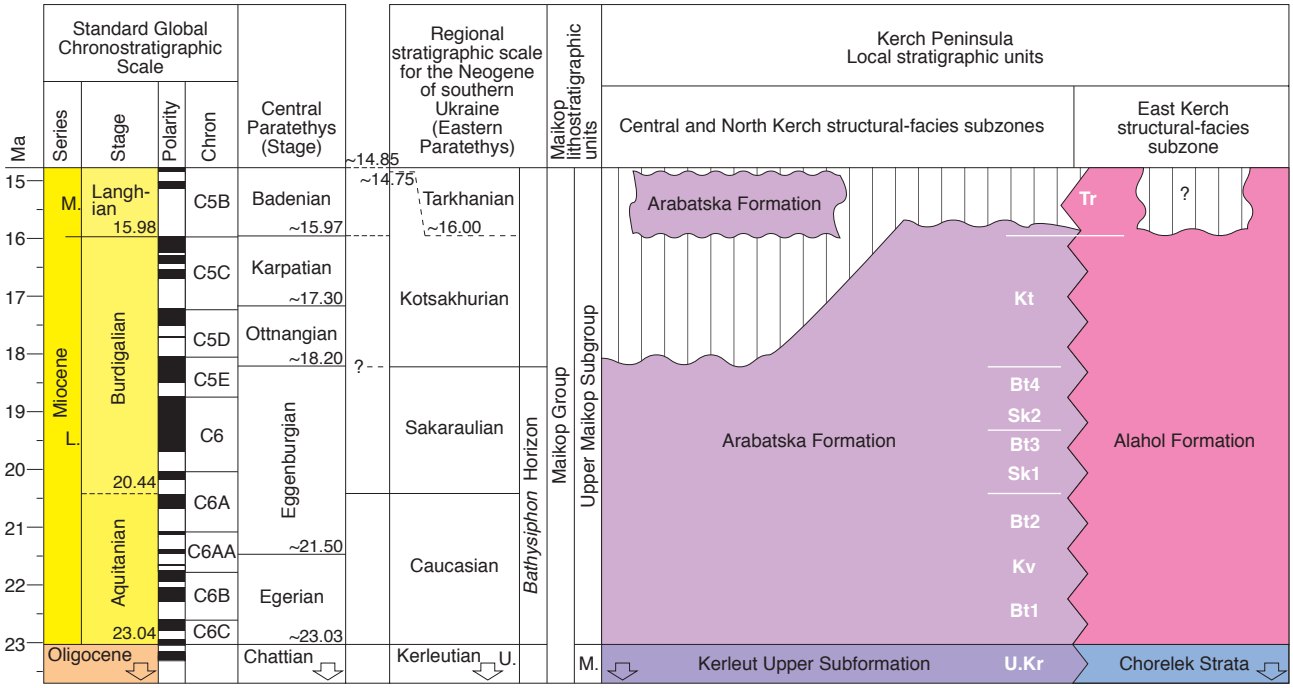


Fig. 4. Stratigraphic framework of the Maikop deposits of the Kerch Peninsula (Upper Kerleutian–Tarkhanian; upper Oligocene – Middle Miocene). Stratigraphic framework after Vernyhorova (2014), Raffi et al. (2020), Vernyhorova et al. (2023). Assemblages of the Maikop deposits (Upper Kerleutian–Tarkhanian, Kerch Peninsula): U.Kr – *Haplophragmoides kerleuticus* assemblage; Cs – *Haplophragmoides periferoexcavata* assemblage; Sk1 – *Cyclammina* assemblage; Sk2 – Calcareous foraminifera assemblage; Kt – *Saccammina zuramakensis* assemblage; Tr – Tarkhanian foraminiferal assemblage; Bt1–Bt4 – *Bathysiphon* assemblage.

characterised by the absence of *H. kerleuticus* and by generally smaller test sizes, giving the assemblage a distinctive appearance; representatives of the genus *Bathysiphon* first appear in the Maikop deposits of the Kerch Peninsula (after Kozyreva's reports, 1949).

- *Cyclammina* assemblage and Calcareous foraminiferal assemblage: Arabatska Formation (Sakaraulian), stratigraphic thickness up to 150 m; archival reports note a prevalence of agglutinated species, in particular representatives of the genus *Cyclammina*, while calcareous taxa become increasingly common toward the upper part of the interval, locally forming mixed assemblages; however, they may be absent in some sections (after Kozyreva's reports, 1949).
- Calcareous foraminiferal assemblage: Arabatska Formation (Sakaraulian), stratigraphic thickness 80–120 m; agglutinated taxa are rare and occur in low specimen numbers, whereas *Bulimina* is frequently reported as the dominant component of the assemblage (after Kozyreva's reports, 1949).
- *Saccammina zuramakensis* assemblage: Arabatska Formation (Kotsakhurian), stratigraphic thickness 300–700 m; represented by a monospecific assemblage of *Saccammina zuramakensis* (Vernyhorova & Ryabokon 2018).
- Tarkhanian foraminiferal assemblage: upper parts of the Arabatska and Alahol formations (Tarkhanian), stratigraphic thickness 15–30 m (Andrusov 1889); characteristic benthic foraminiferal assemblage marking the final stage of the evolution of the Maikop Basin in the Kerch Peninsula sector (Andrusov 1918; Vernyhorova et al. 2023); characterised by a sharp increase in calcareous taxa, whereas agglutinated forms are very sporadic and represented by only a few specimens (Vernyhorova et al. 2023).

Results

Benthic foraminiferal assemblages and their transitions

Haplophragmoides kerleuticus assemblage (U.Kr)

The assemblage comprises 24 taxa of 17 genera, with agglutinated taxa constituting 79 % of the recorded taxa richness (Figs. 5, 6). In addition to the prevalent species *H. kerleuticus*, representatives of the genera *Saccammina*, *Reophax*, and *Ammobaculites* are present. Calcareous foraminifera (Fig. 5) are represented by infaunal taxa: *Uvigerinella* sp., *Nonion* spp., *Elphidium* spp. (?), and epifaunal: *Ammonia* sp., *Cibicides* spp. (e.g., Rosoff & Corliss 1992; Báldi 2006; Murray 2006).

Haplophragmoides periferoexcavata assemblage (Cs)

The foraminiferal assemblage includes 27 taxa of 23 genera, where agglutinated taxa represent 74 % of the assemblage taxa

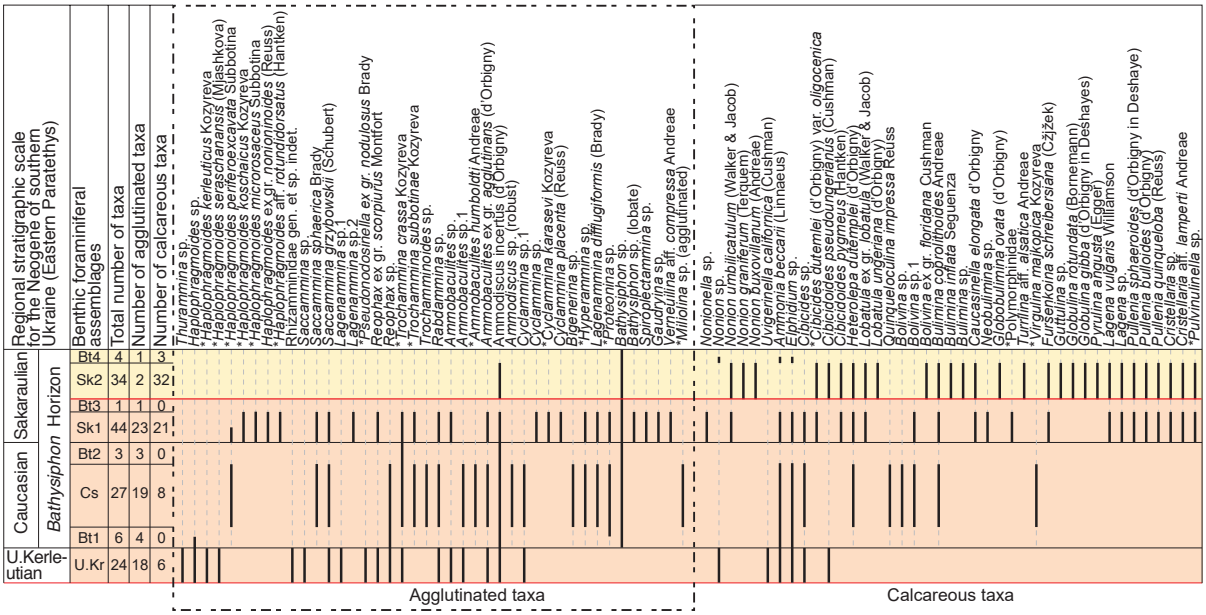


Fig. 5. Distribution of benthic foraminiferal taxa during the Late Kerleutian–Sakaraulian (late Oligocene–Lower Miocene) in the Maikop deposits of the Kerch Peninsula. Colours indicate the shift from agglutinated to calcareous taxa dominance.

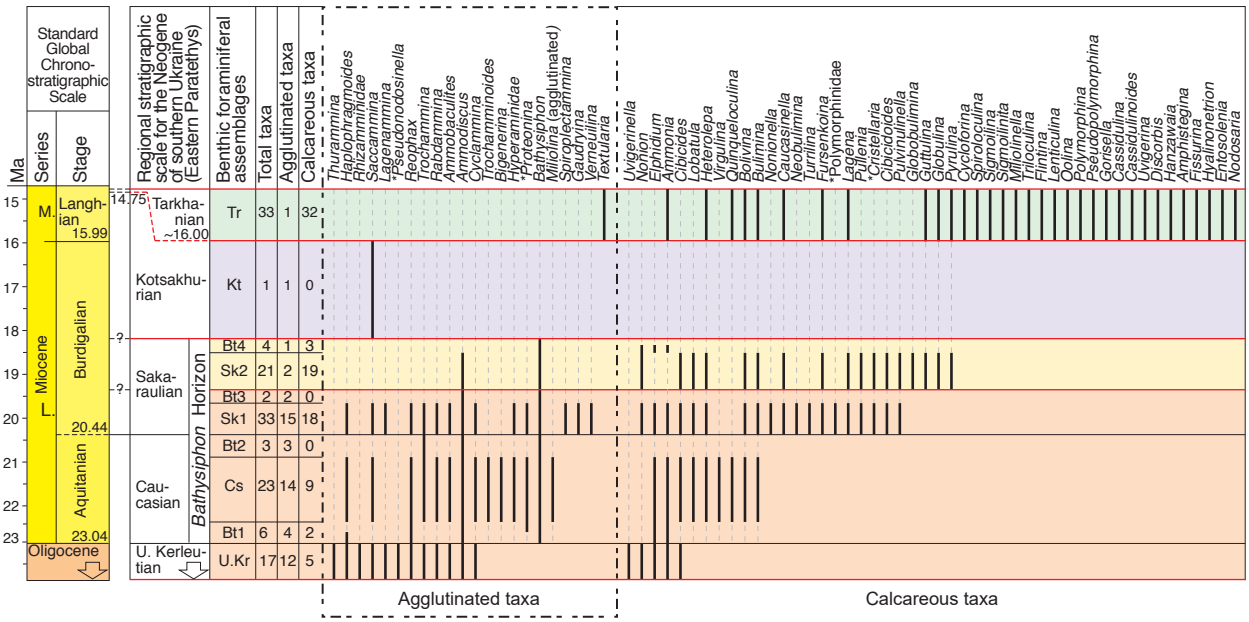


Fig. 6. Distribution of benthic foraminiferal taxa during the Late Kerleutian–Tarkhanian (late Oligocene–Middle Miocene) in the Maikop deposits of the Kerch Peninsula. Colours indicate the shift from agglutinated to calcareous taxa dominance. Stratigraphic framework following Vernyhorova (2014), Raffi et al. (2020), Vernyhorova et al. (2023).

richness (Figs. 5, 6). The taxa composition remains similar to that of the *H. kerleuticus* assemblage. Representatives of agglutinated genera *Bathysiphon*, *Trochamminoides*, *Bigenerina*, and *Proteonina*, as well as taxa of the family Hyperamminidae, also occur in these deposits. Calcareous foraminifera (Fig. 5) are represented by infaunal taxa of the genera: *Bolivina*, *Bulimina*, *Virgulina*, *Elphidium* (infaunal/epifaunal), and epifaunal: *Ammonia*, *Cibicides*, *Lobatula*, *Heterolepa* (predominantly epifaunal), and *Quinqueloculina* (e.g., Rosoff & Corliss 1992; Báldi 2006; Murray 2006).

Cyclammina assemblage (Sk1)

The assemblage comprises 44 taxa of 33 genera, with agglutinated forms accounting for 59 % of the total taxa richness (Figs. 5, 6). Representatives of the genus *Cyclammina* appear

and prevail within the agglutinated group, while the taxonomic diversity of *Haplophragmoides*, *Saccammina*, *Reophax*, *Ammobaculites*, *Ammodiscus*, *Bathysiphon*, *Trochammina*, and *Proteonina* increases. Calcareous foraminifera (Fig. 5) are represented by infaunal taxa: *Nonionella*, *Caucasinella*, *Neobulimina*, *Turrilina*, *Pullenia*, *Lagena*, *Cristellaria*, and *Pulvulinella* (e.g., Rosoff & Corliss 1992; Báldi 2006; Murray 2006).

Calcareous foraminifera assemblage (Sk2)

The assemblage comprises 34 taxa of 21 genera, where agglutinated forms constitute only 6 % of the total taxa richness (Figs. 5, 6). Agglutinated taxa are represented exclusively by *Ammodiscus* and *Bathysiphon*, while the calcareous taxa (Fig. 5) are represented by infaunal: *Globobulimina*, *Guttulina*, *Globulina*, *Pyrulina* (e.g., Rosoff & Corliss 1992; Báldi 2006; Murray 2006).

Bathysiphon assemblage (Bt1–Bt4)

The assemblage comprises 6 taxa of 6 genera, where agglutinated taxa represent 67 % of the total taxa richness (Figs. 5, 6). The assemblage features an extremely impoverished foraminiferal composition, in which the tests of *Bathysiphon* are often the only ones recorded (Kozyreva's reports, 1948, 1949; Maimin 1951). Occasionally, rare specimens of the agglutinated genera *Haplophragmoides*, *Trochammina*, and *Ammodiscus* occur at the base or top of these intervals. However, they remain scarce and disappear quickly. Calcareous foraminifera taxa are represented by eurybiontic taxa: *Ammonia* and *Elphidium* (e.g., Rosoff & Corliss 1992; Báldi 2006; Murray 2006). These so-called "*Bathysiphon* strata" (Kozyreva's reports, 1948, 1949; Maimin 1951) are recorded in the Arabatska Formation (Caucasian–Sakaraulian) on the Kerch Peninsula (Figs. 4, 5, 6).

Saccammina zuramakensis assemblage (Kt)

The assemblage comprises a single agglutinated species, *Saccammina zuramakensis* (Fig. 6).

Tarkhanian foraminiferal assemblage (Tr)

The assemblage comprises 71 taxa of 33 genera, where calcareous forms constitute 99 % of the total taxa richness, with only one agglutinated genus, *Textularia*, being recorded (Fig. 6). Foraminiferal taxa richness and composition are described in detail by Vernyhorova et al. (2023). Calcareous benthic foraminifera (after Rosoff & Corliss 1992; Báldi 2006; Murray 2006) are represented by epifaunal taxa constituting 60 % of the calcareous taxa richness: families Miliolidae (31 taxa), Lagenidae (3 taxa), Lenticulinidae (4 taxa), Nodosariidae (1 taxon), and Amphisteginidae (1 taxon); infaunal calcareous taxa accounting for 31.4 % of the taxa richness: families Bolivinidae (8 species), Polymorphinidae (4 taxa), Guttulinidae (6 taxa), Globulinidae (4 species), Fursenkoinidae (1 taxon), and Cassidulinidae (1 taxon), Nonionidae (1 taxon); and eurybiontic taxa occupying an intermediate position between epifaunal and infaunal (Fig. 7): *Ammonia*, *Elphidium*, *Hanzawaia*, and *Discorbis* (5 taxa in total) (e.g., Báldi 2006; Murray 2006).

Taxonomic structure and diversity trends of benthic foraminifera

In order to identify temporal patterns in benthic foraminiferal assemblages of the Maikop Basin in the Kerch Peninsula sector during the Late Kerleutian–Tarkhanian, statistical analyses of assemblage similarity, taxa richness, and agglutinated morphogroup composition were performed.

Comparative analysis of the unconstrained similarity dendrogram (Fig. 8) and the dendrogram constructed with stratigraphic constraints (Fig. 9)

Analysis of the unconstrained similarity dendrogram (cluster analysis based on the Jaccard coefficient and the paired-group (UPGMA) clustering algorithm) revealed groups of benthic foraminiferal assemblages according to taxonomic similarity, irrespective of their stratigraphic position (Fig. 8). At a low level of overall similarity (J<0.5), five hierarchical clusters are distinguished.

The first cluster (minimum of agglutinated taxa) combines the *Bathysiphon* assemblages (Bt1–Bt4) (Figs. 5, 6). The moderate similarity (J≈0.2–0.4) confirms the recurrence of taxonomic impoverishment of assemblages at different stratigraphic levels during the Caucasian and Sakaraulian.

The second cluster (prevalence of agglutinated taxa) reflects the similarity of benthic foraminiferal assemblages from the Late Kerleutian (U.Kr), Caucasian (Cs), and Sakaraulian (its lower part, Sk1) (Fig. 5). The moderate degree of similarity (J≈0.2–0.4) indicates taxonomic continuity between late Oligocene and Early Miocene assemblages.

The third cluster (prevalence of calcareous taxa, biotic inversion) isolates the benthic foraminiferal assemblage from

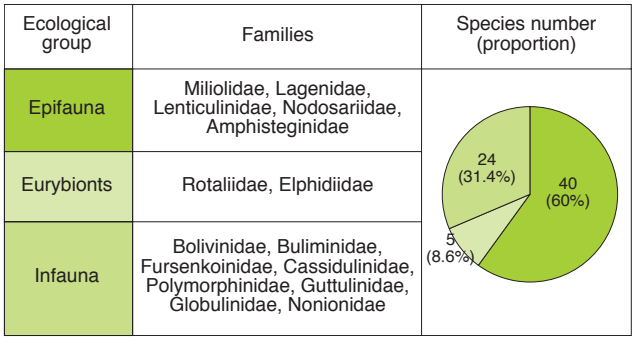
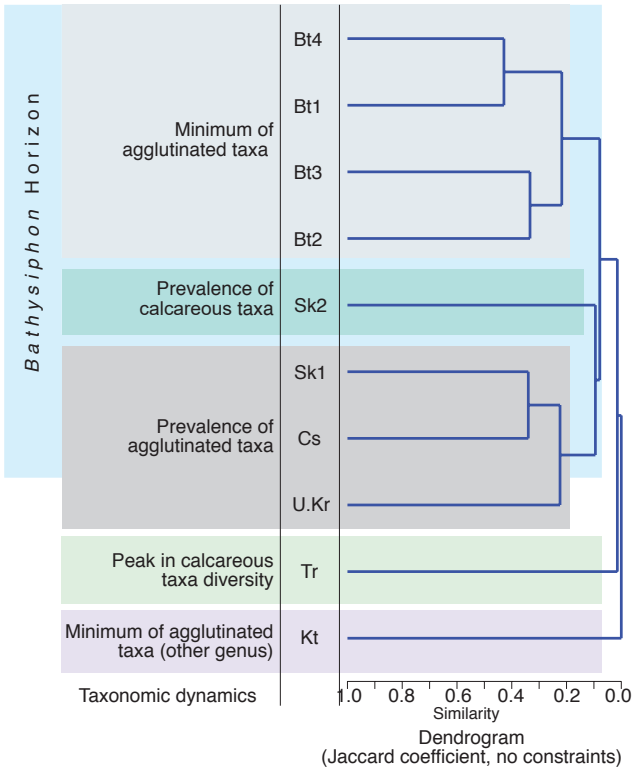
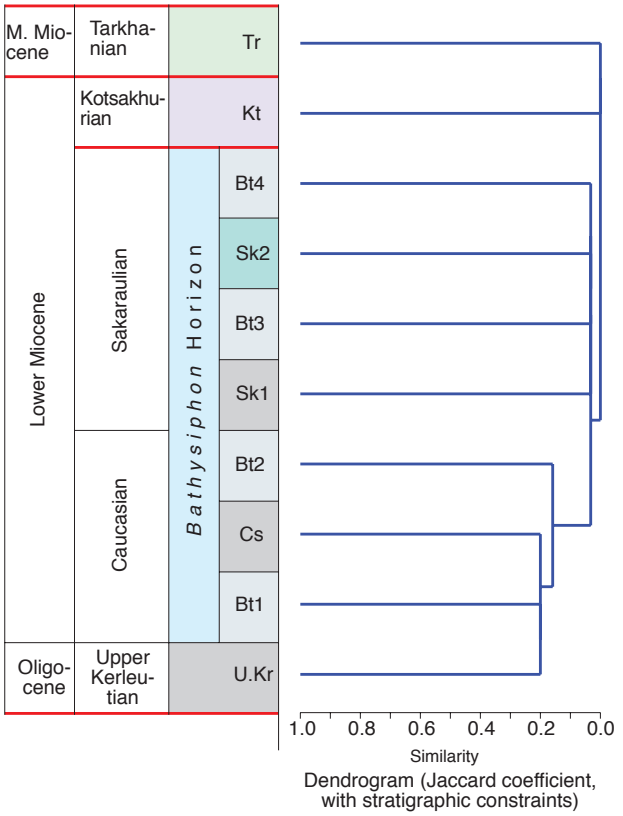


Fig. 7. Ecological group composition of calcareous benthic foraminifera in the Tarkhanian deposits of the Kerch Peninsula (from Vernyhorova et al. 2023).



U.Kr – *Haplophragmoides kerleuticus* assemblage;
Cs – *Haplophragmoides periferoexcavata* assemblage;
Sk1 – *Cyclammina* assemblage;
Sk2 – Calcareous foraminifera assemblage;
Kt – *Saccammina zuramakensis* assemblage;
Tr – Tarkhanian foraminiferal assemblage;
Bt1, Bt2, Bt3, Bt4 – *Bathysiphon* assemblage

Fig. 8. Similarity dendrogram (Jaccard coefficient, the paired-group (UPGMA) clustering algorithm, no stratigraphic constraints) of benthic foraminiferal assemblages from the Maikop deposits of the Kerch Peninsula (Upper Kerleutian–Tarkhanian; upper Oligocene–Middle Miocene). The diagram illustrates the degree of taxonomic similarity between foraminiferal assemblages ranging from Late Kerleutian to Tarkhanian age and their clustering irrespective of stratigraphic position. See legend for assemblage abbreviations.



U.Kr – *Haplophragmoides kerleuticus* assemblage;
Cs – *Haplophragmoides periferoexcavata* assemblage;
Sk1 – *Cyclammina* assemblage;
Sk2 – Calcareous foraminifera assemblage;
Kt – *Saccammina zuramakensis* assemblage;
Tr – Tarkhanian foraminiferal assemblage;
Bt1, Bt2, Bt3, Bt4 – *Bathysiphon* assemblage

Fig. 9. Similarity dendrogram (Jaccard coefficient, the paired-group (UPGMA) clustering algorithm, with stratigraphic constraints) of benthic foraminiferal assemblages from the Maikop deposits of the Kerch Peninsula (Upper Kerleutian–Tarkhanian; upper Oligocene–Middle Miocene). It illustrates the degree of taxonomic similarity between assemblages ranging from Late Kerleutian to Tarkhanian age and their grouping in accordance with stratigraphic position. Colour fill as in Fig. 8. See legend for assemblage abbreviations.

the upper part of the Sakaraulian (Sk2) (Figs. 5, 6). Its low similarity (J<0.2) to the adjacent agglutinated assemblages (U.Kr, Cs, and Sk1) indicates its taxonomic uniqueness and the abrupt nature of the first taxonomic inversion.

The fourth cluster (agglutinated taxa minimum, other genus) isolates the benthic foraminiferal assemblage of Kotsakhurian age (Kt) (Fig. 6). Its extremely low similarity (J≈0.0) to other assemblages reflects a drastic change in taxonomic composition.

The fifth cluster (peak in calcareous taxa diversity) isolates the benthic foraminiferal assemblage of Tarkhanian age (Tr) (Fig. 6). Its extremely low similarity (J≈0.0) to other assemblages also reflects a sharp change in taxonomic composition.

Analysis of the dendrogram with stratigraphic constraints (cluster analysis based on the Jaccard coefficient, the paired-group (UPGMA) clustering algorithm) revealed the temporal changes in benthic foraminiferal assemblages and the degree of their similarity through time (Fig. 9). At a low level of overall similarity (J<0.3), three hierarchical clusters are distinguished in the section.

The first cluster (Late Kerleutian–Caucasian) combines *Haplophragmoides kerleuticus* (U.Kr), first *Bathysiphon* (Bt1), *Haplophragmoides periferoexcavata* (Cs), and second *Bathysiphon* (Bt2) assemblages. The relatively close similarity (J≈0.2) reflects continuity of foraminiferal assemblages across the Oligocene–Miocene boundary.

The second cluster (Sakaraulian) includes *Cyclammina* (Sk1), third *Bathysiphon* (Bt3), Calcareous foraminifera (Sk2), and fourth *Bathysiphon* (Bt4) assemblages. Despite decreasing similarity (J<0.1), the assemblages remain linked within the same stratigraphic succession.

The third cluster (Kotsakhurian–Tarkhanian) includes *Saccammina zuramakensis* (Kt) and Tarkhanian foraminifera

(Tr) assemblages. This cluster shows the lowest similarity to the others (J≈0.0), reflecting a significant difference in taxonomic composition at these stratigraphic levels.

The unconstrained clustering (Fig. 8) reflects taxonomic similarity of benthic foraminiferal assemblages regardless of their position in the section, whereas the application of stratigraphic constraints (Fig. 9) makes it possible to trace the temporal sequence of their changes. Comparison of both dendrograms shows that, although Sk2 is taxonomically distinct in the unconstrained analysis, it remains associated with Sk1 within the stratigraphically constrained succession.

In contrast to the unconstrained dendrogram, the stratigraphically constrained dendrogram demonstrates the overall trend of foraminiferal assemblage changes through time: it records the continuity of assemblages during the late Kerleutian–Sakaraulian, the recurrent appearance of impoverished *Bathysiphon* assemblages, and the sharp separation of the Kotsakhurian and Tarkhanian assemblages. Because stratigraphic constraints force adjacent assemblages to be clustered according to their temporal succession, the resulting dendrogram emphasises overall evolutionary continuity rather than the full extent of taxonomic differentiation. Consequently, the contrast between the *Bathysiphon* crises (Bt1–Bt4) and adjacent assemblages, as well as the distinctiveness of Sk2 relative to Sk1, becomes less pronounced than in the unconstrained analysis (see Figs. 5, 6 for comparison).

Taxa richness and taxonomic proportions of benthic foraminiferal assemblages

Analysis of changes in taxa richness (Taxa_S) and in the taxonomic proportions of agglutinated and calcareous benthic foraminifera, expressed as percentages of the total taxa richness (Fig. 10), revealed the temporal dynamics of benthic foraminiferal assemblage changes.

Total taxa richness (Taxa_S) is minimal (1–3 taxa) in all *Bathysiphon* (Bt1–Bt4) and in *Saccammina zuramakensis* (Kt) assemblages. Moderate taxa richness (20–44 taxa) characterises the Late Kerleutian–Sakaraulian assemblages (U.Kr, Cs, Sk1, Sk2). A peak in taxa richness (71 taxa) is recorded exclusively in the Tarkhanian assemblage (Tr) (Fig. 10A).

The taxonomic proportions of agglutinated and calcareous taxa within each assemblage (Fig. 10B) indicate prevalence of agglutinated taxa during the late Oligocene–Early Miocene. Two peaks in the proportion of calcareous taxa (94 % and 99 %) are recorded in the second half of the Sakaraulian (Sk2) and in the Tarkhanian (Tr), respectively.

Temporal changes in the relative taxonomic proportions of agglutinated and calcareous taxa (Fig. 10C) demonstrate pronounced shifts across the studied interval.

Similarity matrix of taxonomic composition of assemblages

In order to assess the taxonomic similarity of benthic foraminiferal assemblages in the Late Kerleutian–Tarkhanian succession on the Kerch Peninsula, and to further evaluate the patterns observed in the cluster analyses (Figs. 8, 9) and taxonomic characteristics (Fig. 10), a similarity matrix was used (Fig. 11). It reflects the degree of taxonomic similarity between pairs of benthic foraminiferal assemblages (from 0 to 1, where 1 indicates identical taxonomic composition).

Similarity values between the *Bathysiphon* assemblages (Bt1–Bt4) range from 0.167 to 0.429. This is related to the presence, in addition to the nominal genus, of a limited number of specimens of the genera *Haplophragmoides*, *Reophax*, *Ammodiscus*, *Ammonia*, and *Elphidium* in their lower and upper parts (Figs. 5, 6).

The *Haplophragmoides kerleuticus* assemblage (U.Kr) shows a similarity value of 0.275 with the *Haplophragmoides periferoexcavata* assemblage (Cs) and 0.172 with the *Cyclammina* assemblage (Sk1).

The *Haplophragmoides periferoexcavata* assemblage (Cs) shows similarity values of 0.340 with the *Cyclammina* assemblage (lower part of the Sakaraulian, Sk1) and 0.074 with the Calcareous foraminifera assemblage (upper part of the Sakaraulian, Sk2).

The similarity value between the lower and upper parts of the Sakaraulian (Sk1 and Sk2) is 0.172, indicating a significant taxonomic turnover between the *Cyclammina* assemblage and the Calcareous foraminifera assemblage.

Zero similarity was recorded between the *Saccammina zuramakensis* assemblage (Kt) and all other assemblages, reflecting its complete taxonomic isolation.

The Tarkhanian foraminiferal assemblage (Tr) is characterised by similarity values close to zero relative to all other assemblages (mostly <0.05), indicating its pronounced taxonomic isolation. Despite the prevalence of calcareous taxa in both Sk2 and Tr, these two assemblages are taxonomically distinct (similarity value = 0.030).

Morphogroup analysis of agglutinated benthic foraminiferal assemblages

In order to reconstruct the paleoecological conditions of the basin, agglutinated foraminiferal taxa were assigned to functional morphogroups (M) based on test morphology and life-position preferences (Kaminski & Gradstein 2005). Six principal morphogroups were identified, reflecting general feeding strategies and microhabitat preferences (Fig. 12). The ecological characteristics presented below are generalised because the ecological preferences of individual taxa may vary under different environmental conditions (e.g., Murray et al. 2011).

M1 – Tubular: epifaunal to semi-epifaunal (mainly sessile, vertically-oriented forms; passive suspension feeders); characteristic of deep-water (bathyal) settings; representative genera: *Bathysiphon*, *Hyperammina*, *Rhabdammina*, Rhizamminidae (Kaminski & Gradstein 2005). Ecological characteristics: tolerant of reduced oxygen conditions (dysoxia), low competition, and unstable substrates; typically associated with oligotrophic to mesotrophic conditions with low to moderate organic-matter flux; require relatively calm hydrodynamic

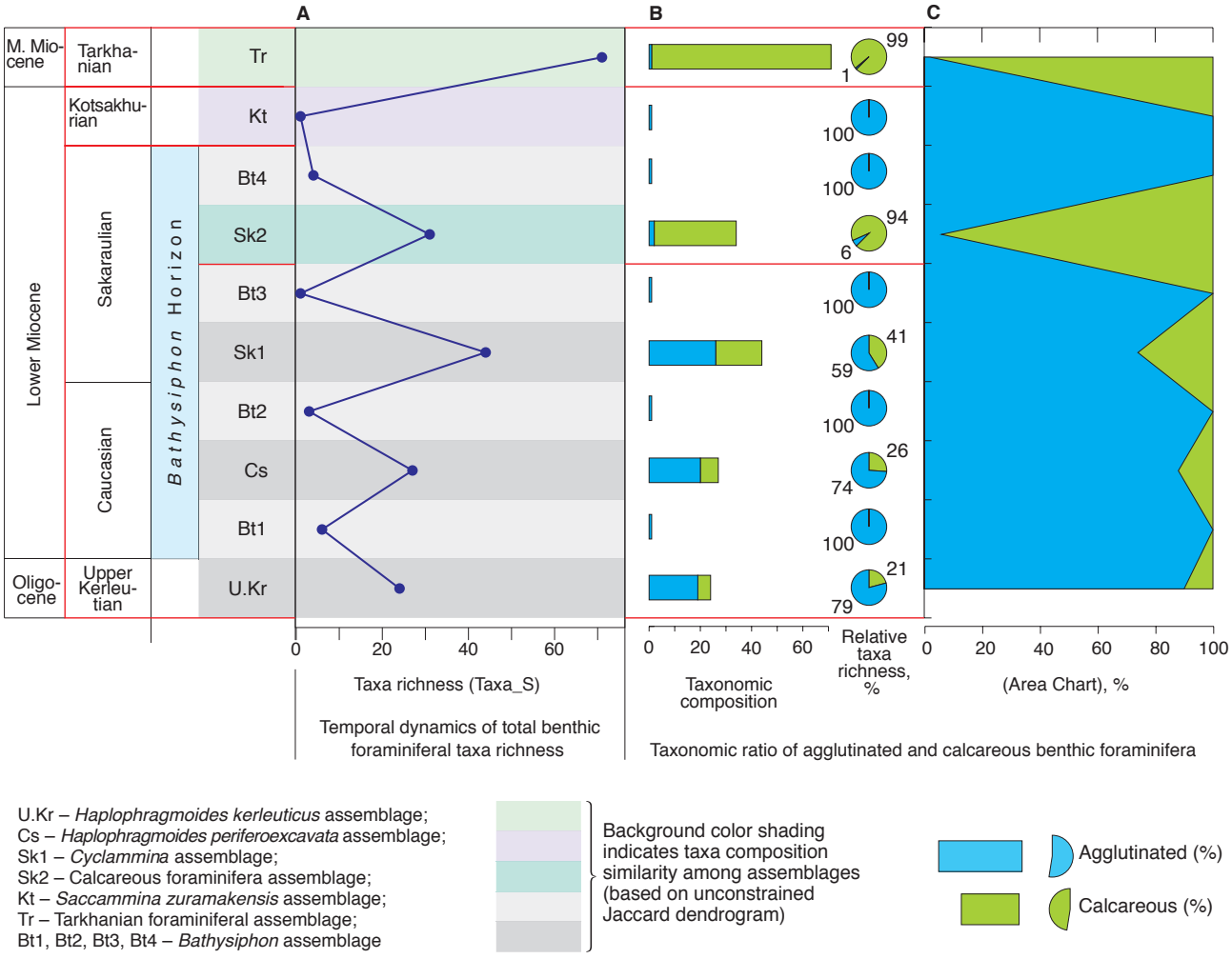


Fig. 10. Taxa richness and taxonomic proportions of agglutinated and calcareous benthic foraminifera in the assemblages from the Maikop deposits of the Kerch Peninsula (Upper Kerleutian–Tarkhanian; upper Oligocene–Middle Miocene). **(A)** Variation in total taxa richness (Taxa_S index); **(B)** taxonomic proportions of agglutinated and calcareous taxa expressed as percentages of total taxa richness; **(C)** temporal changes in the taxonomic proportions of agglutinated and calcareous taxa (100 % stacked area chart). Colour shading indicates: (1) the major stages recognised in the stratigraphically-unconstrained cluster analysis (Fig. 8); (2) in plots B and C, colours correspond to the legend (blue – agglutinated taxa; green – calcareous taxa). See legend for assemblage abbreviations.

	Tr	Kt	Bt4	Sk2	Bt3	Sk1	Bt2	Cs	Bt1	U.Kr
Tr		0.000	0.014	0.030	0.000	0.027	0.000	0.021	0.013	0.011
Kt	0.000		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Bt4	0.014	0.000		0.029	0.250	0.067	0.167	0.107	0.429	0.120
Sk2	0.030	0.000	0.029		0.032	0.172	0.063	0.074	0.057	0.038
Bt3	0.000	0.000	0.250	0.032		0.023	0.333	0.037	0.167	0.000
Sk1	0.027	0.000	0.067	0.172	0.023		0.068	0.340	0.087	0.172
Bt2	0.000	0.000	0.167	0.063	0.333	0.068		0.111	0.286	0.080
Cs	0.021	0.000	0.107	0.074	0.037	0.340	0.111		0.179	0.275
Bt1	0.013	0.000	0.429	0.057	0.167	0.087	0.286	0.179		0.200
U.Kr	0.011	0.000	0.120	0.038	0.000	0.172	0.080	0.275	0.200	

Fig. 11. Similarity matrix of benthic foraminiferal assemblages (Jaccard index, presence/absence data). The colour gradient (heatmap) represents the degree of taxonomic similarity between assemblage pairs. A value of 1.000 indicates identical taxonomic composition, whereas 0.000 indicates that no taxa are shared between assemblages. Values are rounded to three decimal places.

conditions and are sensitive to intense mechanical disturbance of the sediment; may form monoassociations under ecological stress (Gooday & Pond 2002; Kaminski & Gradstein 2005).

M2 – Globular (single-chambered spherical or sack-like forms): surface infauna/interface dwellers; passive deposit feeders; characteristic of deep-water (bathyal) settings; representative genera: *Saccammina*, *Lagenammina*, *Proteonina* (Kaminski & Gradstein 2005). Ecological characteristics: tolerant of dysoxia; associated with variable organic-matter supply (mesotrophic to eutrophic conditions); capable of colonising disturbed substrates (Kuhnt et al. 1996; Kaminski & Gradstein 2005).

M3a – Planispiral/Discoid: mainly epifaunal, surface gatherers; predominantly shelf environments, representative genera: *Ammodiscus*, *Trochamminoides* (Kaminski & Gradstein 2005). Ecological characteristics: often associated with dysoxia, ecological instability, and transitional conditions; occur in

oligotrophic to mesotrophic settings; can form acmes in periods of environmental change (Kuhnt et al. 1996; Kaminski & Gradstein 2005).

M3b – Planispiral/Lenticular: shallow infaunal (upper sediment layer); mainly inner shelf to upper bathyal; representative genera: *Haplophragmoides*, *Cyclammina* (Kaminski & Gradstein 2005). Ecological characteristics: passive deposit feeders; tolerant of moderate dysoxia; associated with mesotrophic conditions and increased organic-matter flux; characteristic of variable or transitional bottom environments (Kuhnt et al. 1996; Kaminski & Gradstein 2005).

M4 – Trochospiral: epifaunal/surface infaunal; active or semi-active gatherers; predominantly shelf, representative genera: *Trochammina* (Kaminski & Gradstein 2005). Ecological characteristics: sensitive to changes in organic-matter supply; more common in mesotrophic conditions; respond to increased organic-matter flux (Kaminski & Gradstein 2005).

M5 – Uniserial/Elongated: infaunal (mobile forms within the sediment); mainly inner shelf to upper bathyal; representative genera: *Reophax*, *Pseudonodosinella*, *Ammobaculites* (Kaminski & Gradstein 2005). Ecological characteristics: active deposit feeders; tolerant of dysoxia; associated with variable to increased organic-matter flux (mesotrophic to eutrophic conditions) and capable of occurring under conditions of rapid sedimentation (Kuhnt et al. 1996; Kaminski & Gradstein 2005).

M6 – Multichambered/Textulariid: infaunal (shallow to intermediate); mainly shelf to upper bathyal; representative genera: *Textularia*, *Spiroplectammina*, *Gaudryina*, *Bigenerina*, *Verneuilina*, agglutinated miliolids (Kaminski & Gradstein 2005). Ecological characteristics: deposit feeders; tolerant of reduced oxygen (dysoxia); associated with mesotrophic to eutrophic conditions and moderate to increased organic-matter supply; occur in variable bottom environments (Kuhnt et al. 1996; Kaminski & Gradstein 2005).

The taxonomic proportions of morphogroups (Fig. 12) reveal significant heterogeneity among assemblages throughout the section. Assemblages with low agglutinated taxa richness – the *Haplophragmoides kerleuticus* assemblage (U.Kr; 16 agglutinated taxa), the *Haplophragmoides periferoexcavata* assemblage (Cs; 19 agglutinated taxa), and the *Cyclammina* assemblage (Sk1; 27 agglutinated taxa) – are characterised by the presence of all morphogroups, with M3b (up to 30 %), M2 (up to 21 %), and M5 (up to 31 %) showing the highest taxonomic proportions. The remaining assemblages are represented by only one or two morphogroups:

- Calcareous foraminifera assemblage (Sk2; 2 agglutinated taxa): one taxon each from morphogroups M1 and M3a;
- *Bathysiphon* assemblage (Bt1–Bt4): with rare additional taxa occurring only in the lowermost samples and disappearing rapidly upward; above this level, the assemblage becomes monospecific (*Bathysiphon*);
- *Saccammina zuramakensis* assemblage (Kt; 1 agglutinated taxon): morphogroup M2 (monospecific association);
- Tarkhanian foraminifera assemblage (Tr; 1 agglutinated taxon): morphogroup M6.

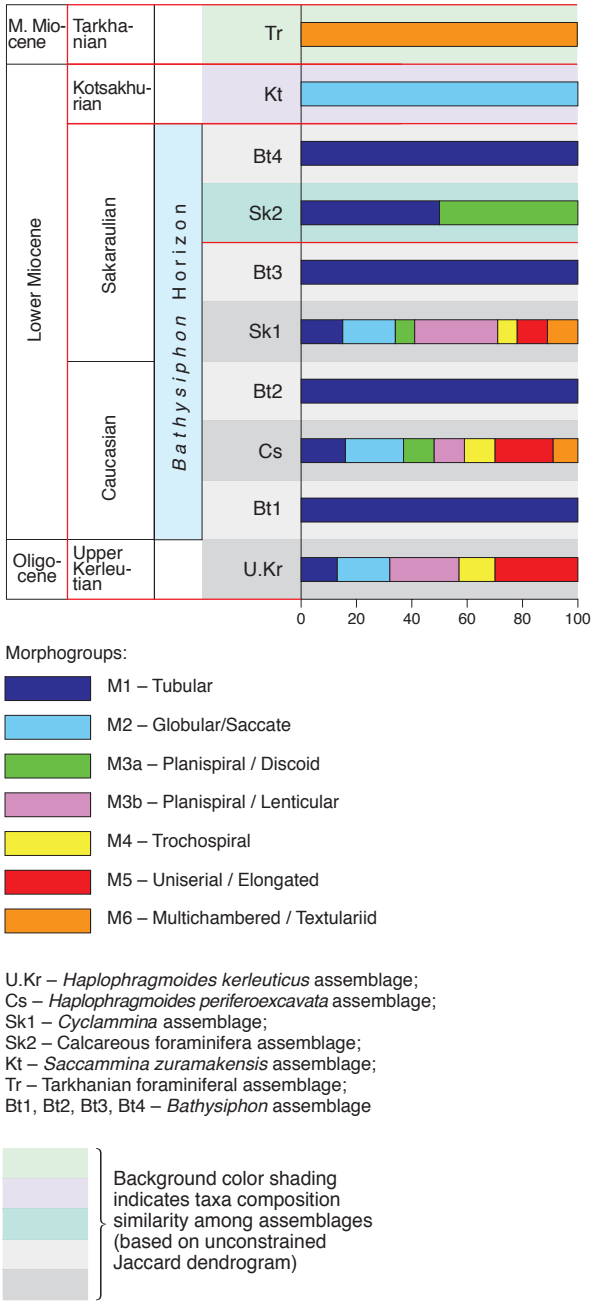


Fig. 12. Morphogroup distribution of agglutinated benthic foraminifera during the Late Kerleutian–Tarkhanian (late Oligocene–early Middle Miocene) in the Maikop deposits of the Kerch Peninsula. 100 % stacked bar chart. See legend for assemblage abbreviations.

Discussion

Dynamics and ecological reorganisation of benthic foraminiferal assemblages (Late Kerleutian–Tarkhanian)

The Late Kerleutian–Tarkhanian benthic foraminiferal succession from the Kerch Peninsula sector of the Maikop Basin is characterised by repeated alternation of persistent assemblages, biotic crises, and taxonomic inversions.

Persistent agglutinated phase

Taxonomic affinity and continuity among the *Haplophragmoides kerleuticus* (U.Kr), *H. periferoexcavata* (Cs), and *Cyclammina* (Sk1) assemblages indicate a prolonged phase of relative stability in benthic foraminiferal assemblage structure during the Late Kerleutian, Caucasian, and early Sakaraulian (Figs. 5, 6, 8, 9, 13). Throughout this interval, agglutinated taxa consistently dominate (74–79 % of the recorded taxa richness), while nearly the complete spectrum of morphogroups (M1–M6) remains represented. Functionally, these assemblages are dominated by representatives of morphogroups M3b (planispiral lenticular: *Haplophragmoides*, *Cyclammina*), M2 (spherical: *Saccammina*, *Lagenammina*, *Proteonina*), and M5 (uniserial: *Reophax*, *Pseudonodosinella*, *Ammobaculites*) (Fig. 12).

The observed differences between these assemblages are limited primarily to changes in individual taxa and genera, including the first appearance of *Bathysiphon* (M1) in the Caucasian deposits (Figs. 5, 6). At the same time, the overall taxonomic structure remains remarkably consistent. Within the calcareous component, infaunal taxa predominate, represented mainly by the families Bolivinidae (*Bolivina*), Buliminidae (*Bulimina*, *Globobulimina*), Nonionidae (*Nonionella*), and Polymorphinidae (*Guttulina*, *Globulina*, *Pyrulina*), among others (Fig. 7). Despite a gradual increase in taxonomic richness within both agglutinated and calcareous groups, the overall organisation of the assemblages remained remarkably stable, suggesting long-term persistence of the same benthic assemblage structure (Figs. 5, 6).

Event (assemblage dynamics)	Characteristic of assemblage	Stratigraphic interval (assemblage)	Taxonomic structure
Persistent agglutinated phase	Prevalence of agglutinated taxa. Moderate diversity (18, 27, 44 spp.). Stable assemblage core	Upper Kerleutian – Caucasian (U.Kr, Cs)	Prevalence of agglutinated taxa; M2-M3 semi-infaunal morphogroups
		lower Sakaraulian (Sk1)	Prevalence of M2-M3 semi-infaunal morphogroups increased taxa richness
Recurrent *Bathysiphon* crises	Agglutinated minimum. Taxonomic crisis (up to 5 spp.). Recurrent assemblages	Caucasian – Sakaraulian (Bt1-Bt4)	Prevalence of the M1 morphogroup (sessile epifauna or semi-epifauna)
Saccammina crisis	Agglutinated minimum. Taxonomic crisis (single species). Recolonization phase	Kotsakhurian (Kt)	M2 semi-infaunal morphogroup only
First calcareous inversion	Inversion: replacement of agglutinated assemblages by calcareous ones (31 spp.)	upper Sakaraulian (Sk2)	Prevalence of calcareous taxa; agglutinated M1 and M3 morphogroups
Second calcareous inversion	Inversion: replacement of agglutinated assemblages by calcareous ones (71 spp.)	Tarkhanian (Tr)	Prevalence of calcareous taxa; M6 infaunal morphogroup; peak taxa richness

U.Kr – *Haplophragmoides kerleuticus* assemblage;
Cs – *Haplophragmoides periferoexcavata* assemblage;
Sk1 – *Cyclammina* assemblage;
Sk2 – Calcareous foraminifera assemblage;
Kt – *Saccammina zuramakensis* assemblage;
Tr – Tarkhanian foraminiferal assemblage;
Bt1, Bt2, Bt3, Bt4 – *Bathysiphon* assemblage

Fig. 13. Synthesis of benthic foraminiferal assemblage dynamics and ecological reorganisation during the Late Kerleutian–Tarkhanian. Background colour shading indicates taxa composition similarity among assemblages based on the unconstrained Jaccard dendrogram (Fig. 8). See legend for assemblage abbreviations.

Recurrent Bathysiphon crises

Recurrent monospecific *Bathysiphon* assemblages (morphogroup M1; Bt1–Bt4) represent the most pronounced episodes of faunal depletion recognised in the Caucasian and Sakaraulian (Figs. 5, 6). These crisis intervals are characterised by the near-exclusive occurrence of *Bathysiphon*, whereas representatives of other genera become extremely rare (Figs. 5, 6, 13). The presence of isolated specimens of *Haplophragmoides*, *Reophax*, *Ammodiscus*, *Ammonia*, and *Elphidium* at the base, and occasionally at the top, of these intervals suggests that these episodes represent rapid phases of assemblage restructuring. The high degree of similarity among the Bt1–Bt4 assemblages (Fig. 11) indicates that they represent repeated expressions of the same faunal response despite occurring at different stratigraphic levels.

First calcareous inversion

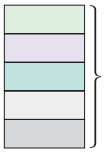
A pronounced taxonomic turnover is recorded during the late Sakaraulian and is expressed by the Calcareous foraminifera assemblage (Sk2) (Figs. 5, 6, 13). This assemblage marks the first major inversion in benthic foraminiferal composition, characterised by a drastic decline in agglutinated taxa (to 6 %; represented only by *Bathysiphon* – M1 and *Ammodiscus* – M3a) and the rapid predominance of calcareous taxa (up to 94 %). Among the latter, infaunal representatives prevail (after Rosoff & Corliss 1992; Murray 2006), including *Globobulimina*, *Guttulina*, *Globulina*, *Pyrulina*, and others (Figs. 5, 6). At the same time, the assemblage shows low taxonomic similarity to all other assemblages recognised in the section (Figs. 10, 11).

Saccammina crisis

Another agglutinated minimum is recognised in the Kotsakhurian and is represented by the monospecific *Saccammina zuramakensis* assemblage (Kt; Figs. 6, 8, 13, 14).

Event (assemblage dynamics)	Stratigraphic interval (assemblage)	Oxygenation conditions	Trophic conditions	Bathymetry and hydrological regime	Biotic response	Supporting references
Persistent agglutinated phase	Upper Kerleutian – Caucasian (U.Kr, Cs)	Suboxic	Mesotrophic	Upper bathyal; normal marine	Persistent agglutinated assemblages with gradual increase in taxonomic richness	e.g., Kuhnt et al. 1996; Nagy et al. 2000; Kaminski & Gradstein 2005
	lower Sakaraulian (Sk1)	Suboxic (improved aeration)	Mesotrophic (increasing resources)			
Recurrent *Bathysiphon* crises	Caucasian – Sakaraulian (Bt1-Bt4)	Suboxic–dysoxic	Low to moderate organic-matter flux (oligotrophic to mesotrophic)	Upper bathyal; restricted bottom-water exchange and reduced ventilation	Recurrent reduction of assemblages to a single-species taxon	e.g., Gooday & Pond 2002; Kaminski & Gradstein 2005
Saccammina crisis	Kotsakhurian (Kt)	Dysoxic (fluctuating oxygenation)	Eutrophic	Transitional bathymetry (bathyal to shelf); unstable marine conditions; episodic hydrodynamic activity	Dominance of a stress-tolerant taxon (monotaxon association)	e.g., Alve 1999; Gooday 2003; Kaminski & Gradstein 2005
First calcareous inversion	upper Sakaraulian (Sk2)	Suboxic (improved ventilation)	Mesotrophic-eutrophic (resource-rich)	Upper bathyal; normal marine	Replacement of agglutinated assemblages by calcareous ones	e.g., Kaiho 1994, 1999; Jorissen et al. 1995; Rosoff & Corliss 1992
Second calcareous inversion	Tarkhanian (Tr)	Oxic-suboxic (improved ventilation)	Mesotrophic (locally eutrophic)	Outer sublittoral normal marine	Expansion of calcareous taxa with extensive taxonomic renewal	e.g., Kaiho 1994, 1999; Jorissen et al. 1995; Rosoff & Corliss 1992; Murray 2006

U.Kr – *Haplophragmoides kerleuticus* assemblage;
Cs – *Haplophragmoides periferoexcavata* assemblage;
Sk1 – *Cyclammina* assemblage;
Sk2 – Calcareous foraminifera assemblage;
Kt – *Saccammina zuramakensis* assemblage;
Tr – Tarkhanian foraminiferal assemblage;
Bt1, Bt2, Bt3, Bt4 – *Bathysiphon* assemblage



Background color shading indicates taxa composition similarity among assemblages (based on unconstrained Jaccard dendrogram)

Fig. 14. Ecological characteristics of benthic foraminiferal assemblages from the Maikop deposits of the Kerch Peninsula (Upper Kerleutian–Tarkhanian; upper Oligocene–Middle Miocene), including taxonomic structure, oxygenation conditions, trophic conditions, hydrological regime, and biotic response. See legend for assemblage abbreviations.

Although this assemblage is comparable to the *Bathysiphon* crises (Bt1–Bt4) in its extremely low taxonomic diversity (Fig. 8), it differs fundamentally by the first appearance of the new taxon *Saccammina zuramakensis* (morphogroup M2), which is absent from the underlying deposits. Both the cluster analysis and the similarity matrix demonstrate the near-zero similarity and marked taxonomic isolation of the *S. zuramakensis* assemblage relative to all other assemblages (Figs. 8, 11). This crisis followed the final *Bathysiphon* episode (Bt4), indicating a distinct phase of faunal reorganisation rather than a recurrence of the preceding *Bathysiphon* crises.

Second calcareous inversion

A second calcareous inversion, which coincides with the highest taxonomic diversity recorded in the succession (71 taxa belonging to 33 genera; Figs. 4, 5, 6, 8, 9, 13), characterises the Tarkhanian. This interval is represented by the Tarkhanian foraminiferal assemblage (Tr), in which calcareous taxa overwhelmingly predominate (99 %). The inversion differs fundamentally from the preceding late Sakaraulian calcareous inversion (Sk2) in both taxonomic richness and taxonomic composition. Unlike the preceding late Sakaraulian Calcareous foraminifera assemblage (Sk2), the Tarkhanian assemblage includes a broad spectrum of both epifaunal and infaunal calcareous taxa, reflecting a substantially more diversified taxonomic structure.

Both the cluster analysis and the similarity matrix demonstrate the isolated position of the Tarkhanian assemblage (Similarity≈0), with uniformly low similarity values (predominantly <0.05) relative to the underlying intervals, including the late Sakaraulian Calcareous foraminifera assemblage

(Tr−Sk2=0.030; Fig. 11). This pattern indicates a profound taxonomic reorganisation and suggests substantial biotic renewal following the Kotsakhurian crisis.

The marked taxonomic differences between the two calcareous inversions indicate that the Tarkhanian represents a distinct phase of benthic foraminiferal reorganisation rather than a simple recurrence of the preceding late Sakaraulian assemblage.

Paleoecological evolution of the Maikop Basin (Late Kerleutian–Tarkhanian) on the Kerch Peninsula sector based on benthic foraminifera

The identified patterns of benthic foraminiferal assemblage reorganisation are interpreted as responses to changes in bottom-water environmental conditions and provide the basis for reconstructing the major phases of the paleoecological evolution of the Maikop Basin in the Kerch Peninsula sector (Fig. 15). Four phases of paleoecological restructuring are recognised during the Late Kerleutian–Tarkhanian.

Late Kerleutian–early Sakaraulian (late Oligocene–Early Miocene)

The persistent agglutinated assemblages (U.Kr, Cs, Sk1) indicate that bottom-water conditions remained relatively stable during the Late Kerleutian–early Sakaraulian (Figs. 13, 14, 15). Their persistent taxonomic composition, dominance of agglutinated taxa, and nearly complete morphogroup spectrum suggest moderate water circulation, predominantly suboxic oxygenation, and mesotrophic conditions at bathyal depths (after Kuhnt et al. 1996; Nagy et al. 2000; Kaminski & Gradstein 2005).

The recurrent *Bathysiphon* crises in the Caucasian–Sakaraulian (Bt1–Bt4) reflect repeated interruptions of this persistent agglutinated phase. The occurrence of monospecific assemblage *Bathysiphon* (morphogroup M1) serves as an indicator of environmental stress and low competition in deep-water settings (Gooday & Pond 2002; Kaminski & Gradstein 2005).

Taken together, these assemblages define the characteristic environmental pattern of this interval, reflecting alternation

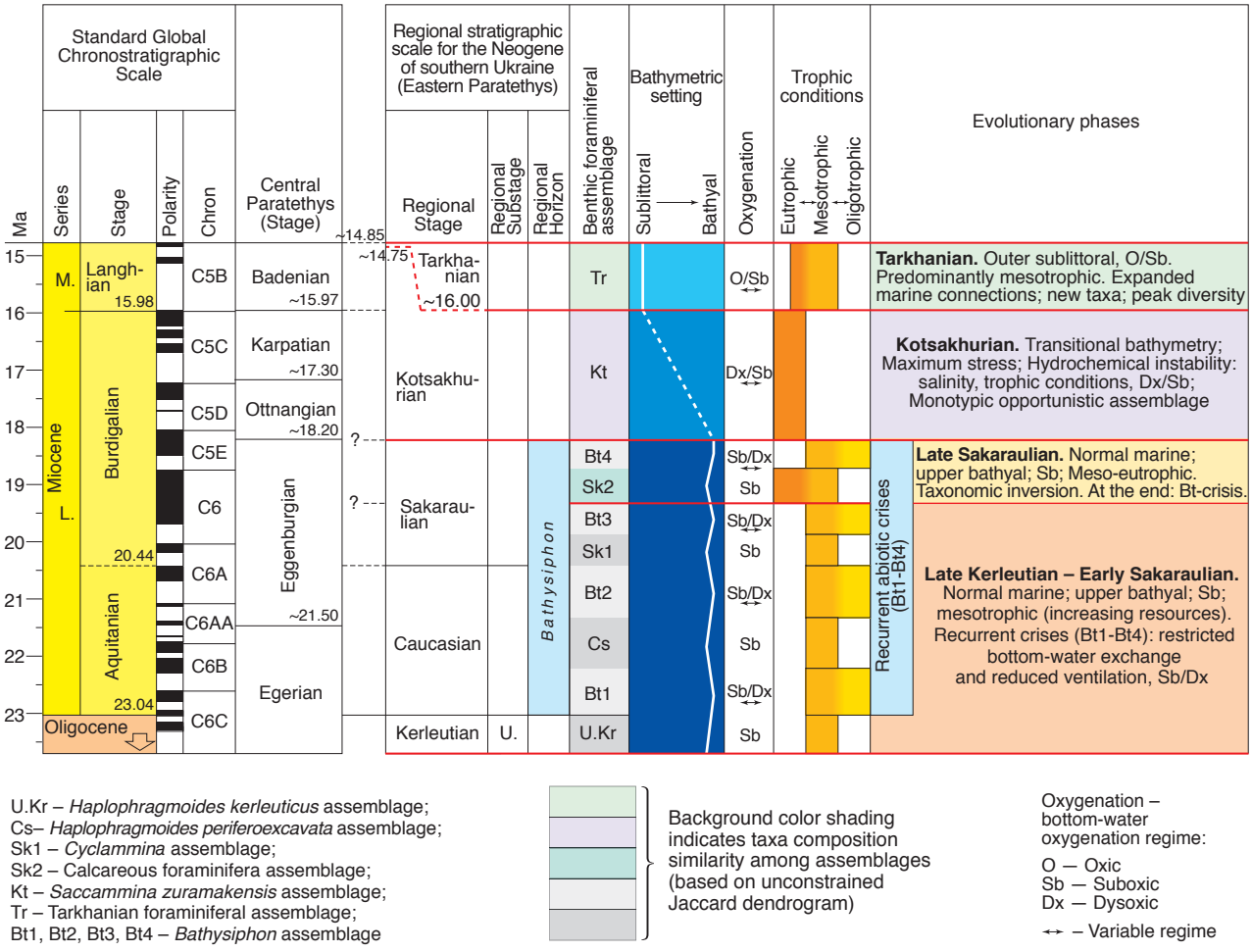


Fig. 15. Paleoecological evolution of the Maikop Basin in the Kerch Peninsula sector (Late Kerleutian–Tarkhanian; late Oligocene–Middle Miocene) based on benthic foraminiferal assemblages. See legend for assemblage abbreviations and oxygenation symbols.

between relatively stable benthic conditions and recurrent episodes of environmental stress. Overall, the Kerch Peninsula sector of the Maikop Basin remained a relatively stable upper-bathyal environment with predominantly suboxic oxygenation and mesotrophic conditions. Progressive growth in taxonomic richness suggests that these conditions gradually became more favourable toward the early Sakaraulian. The repeated recovery of the persistent agglutinated assemblages after each *Bathysiphon* crisis indicates that the benthic ecosystem retained its capacity for recovery despite these environmental disturbances.

Late Sakaraulian (Early Miocene)

The first major taxonomic inversion, represented by the Calcareous foraminifera assemblage (Sk2), occurred immediately after the *Bathysiphon* crisis (Bt3) and marked the late Sakaraulian. This inversion reflects a pronounced improvement in bottom-water conditions compared to the preceding interval of reduced water circulation, resulting in the rapid predominance of calcareous taxa (Figs. 13, 14, 15). Under normal-marine bathyal conditions, bottom waters remained predominantly suboxic, while the supply of organic matter increased to mesotrophic-eutrophic levels. The assemblage is dominated by infaunal representatives of the families Buliminidae and Polymorphinidae, particularly *Globobulimina*, which are widely regarded as indicators of elevated organic-matter flux and moderate oxygen deficiency within the sediment (Rosoff & Corliss 1992; Kaiho 1994, 1999; Jorissen et al. 1995). Therefore, the first calcareous inversion represents a major biotic response to improved bottom-water circulation and enhanced trophic conditions.

This assemblage characteristics indicate that during the late Sakaraulian, the Kerch Peninsula sector of the Maikop Basin experienced a pronounced ecological reorganisation. Enhanced bottom-water circulation under normal-marine bathyal conditions promoted the establishment of calcareous-dominated benthic assemblages, replacing the previously persistent agglutinated assemblages. This interval represents the first major departure from the long-lasting agglutinated phase that had characterised the basin since the Late Kerleutian.

At the end of the Sakaraulian, the final *Bathysiphon* crisis (Bt4) marks the termination of this recurring pattern. Unlike the preceding *Bathysiphon* episodes, after which the stable agglutinated assemblages repeatedly recovered, the post-crisis recovery resulted instead in the establishment of a fundamentally different benthic assemblage. Consequently, *Bathysiphon* disappears from the section, and the previous agglutinated assemblage type is no longer re-established.

Kotsakhurian (Early Miocene)

The establishment of the monospecific *Saccammina zuramakensis* assemblage marks a new stage in the evolution of the Maikop Basin during the Kotsakhurian (Figs. 13, 14, 15). Unlike the preceding *Bathysiphon* crises, this assemblage reflects a fundamentally different type of bottom environmental instability. Representatives of the genus *Saccammina* are stress-tolerant opportunists capable of inhabiting dysoxic settings across a wide trophic range, including eutrophic conditions, while withstanding fluctuating salinity and hydrochemical instability (e.g., Kaminski & Gradstein 2005). The dominance of a single taxon suggests that environmental conditions approached the tolerance limits of most benthic foraminiferal taxa (Alve 1999; Gooday 2003).

These assemblage characteristics indicate that during the Kotsakhurian, the Kerch Peninsula sector of the Maikop Basin was under hydrochemical instability, characterised by fluctuations in salinity, trophic conditions, and bottom-water oxygenation, along with possible episodes of partial basin isolation. Due to the eurybathic nature of *Saccammina* and the lack of other bioindicators, the precise depth of the Kotsakhurian Basin within the Kerch Peninsula remains a subject of debate; however, the overall sequence architecture suggests a transitional position between bathyal (Sakaraulian) and shelf (Tarkhanian) settings.

Deposits containing monospecific assemblage *Saccammina* (*S. zuramakensis, S. ovalis, S. suzini*) are characteristic of the Kotsakhurian across the Eastern Paratethys (e.g., Bogdanovich 1954; Nevesskaya et al. 1975, 1984; Muratov & Nevesskaya 1986). The evolutionary links between these Kotsakhurian taxa and the earlier *Saccammina* taxa found in older deposits remain unclear (Bogdanovich 1954, 1960, 1965). In the Kerch Peninsula section, the last representatives of the genus are recorded in the early Sakaraulian (Fig. 5). Isolated *Saccammina* populations likely persisted in local refugia under relatively favourable conditions, where they underwent further differentiation. This was followed by widespread expansion during the Kotsakhurian under acute environmental stress (dysoxia and salinity fluctuations). Such conditions promoted the dominance of opportunistic forms capable of efficiently utilising high organic matter flux (eutrophic conditions) in the absence of interspecific competition.

Notably, throughout much of the Eastern Paratethys, monospecific *Saccammina* assemblages commonly occur separately from the classical Kotsakhurian mollusk assemblages (e.g., Bogdanovich 1954, 1960). This spatial separation suggests pronounced environmental heterogeneity across the Eastern Paratethys during the Kotsakhurian. Consequently, the observed distribution of these assemblages does not support the concept of uniformly brackish-water conditions throughout the Eastern Paratethys during the Kotsakhurian.

Thus, the Kotsakhurian crisis represents a regional ecological reorganisation recognised throughout much of the Eastern Paratethys, where monospecific *Saccammina* assemblages are widely distributed (e.g., Muratov & Nevesskaya 1986).

Tarkhanian (Middle Miocene)

The second major calcareous inversion recognised in the Tarkhanian foraminiferal assemblage (Tr) represents the most taxonomically diverse benthic assemblage within the studied

Late Kerleutian–Tarkhanian succession (Figs. 13, 14, 15). The overwhelming dominance of calcareous taxa, together with the broad representation of both epifaunal and infaunal groups, indicates a substantially more favourable benthic environment than during the preceding intervals.

These assemblage characteristics indicate that during the Tarkhanian, the Kerch Peninsula sector of the Maikop Basin experienced a major improvement in bottom-water conditions. Basin shallowing toward outer sublittoral settings was accompanied by oxic-suboxic bottom waters and predominantly stable mesotrophic (locally eutrophic) conditions, allowing the establishment of a broader range of ecological niches (Rosoff & Corliss 1992; Kaiho 1994, 1999; Jorissen et al. 1995; Murray 2006) (Figs. 13, 14, 15).

Unlike the late Sakaraulian calcareous inversion, the Tarkhanian assemblage represents not only an increase in the proportion of calcareous taxa but also a profound renewal of their taxonomic composition. The influx of numerous newly-appearing taxa suggests faunal immigration associated with expanded connections between the Eastern Paratethys and adjacent marine basins during the terminal phase of the Miocene Climatic Optimum (Vernyhorova et al. 2023).

Despite this pronounced renewal of benthic assemblages, the characteristic Maikop depositional system has remained unchanged in the Kerch Peninsula sector (e.g., Andrusov 1889, 1918; Vernyhorova et al. 2023). This indicates that the Tarkhanian faunal reorganisation took place during the final stage of Maikop sedimentation.

Comparison with published benthic foraminiferal records from other parts of the Maikop Basin indicates that the succession documented on the Kerch Peninsula combines both regional and locally distinctive features (Bogdanovich 1954, 1960; Djanelidze 1970; Muratov & Nevesskaya 1986; Vernyhorova 2014, 2015, 2016; Vernyhorova & Ryabokon 2018, 2020; Palcu et al. 2019; Vernyhorova et al. 2023). The Kotsakhurian *Saccammina* crisis and the Tarkhanian calcareous renewal can be recognised throughout much of the Eastern Paratethys (Nevesskaya et al. 1975, 1984; Muratov & Nevesskaya 1986), thereby indicating that these represent regional paleoenvironmental events. In contrast, no comparable Upper Kerleutian–Sakaraulian succession combining a prolonged agglutinated phase, recurrent *Bathysiphon* crises, and the first calcareous inversion, has been recognised in other studied parts of the Maikop Basin. The exceptional continuity of the Kerch succession thus provides a unique opportunity to reconstruct the ecological evolution of the Maikop Basin during the late Oligocene–Middle Miocene.

Conclusions

The benthic foraminiferal succession from the Late Kerleutian to the Tarkhanian demonstrates that the paleoecological evolution of the Maikop Basin in the Kerch Peninsula sector was non-linear. Changes in benthic assemblages occurred simultaneously at several hierarchical levels, including variations in assemblage composition, taxonomic richness, taxonomic diversity, and ecological structure. Together, these patterns document the principal stages of environmental reorganisation within the basin.

The main long-term pattern observed across most of the studied area was the continued prevalence of agglutinated taxa in benthic foraminiferal assemblages from the Late Kerleutian through the Caucasian, early Sakaraulian, and Kotsakhurian. Against this background, two major wall-type dominance inversions are recognised. The late Sakaraulian inversion temporarily disrupted the long-term prevalence of agglutinated taxa, whereas the Tarkhanian inversion marked its final termination.

The agglutinated assemblages exhibit their own internal evolutionary dynamics. During the Late Kerleutian, Caucasian, and early Sakaraulian, relatively diverse agglutinated assemblages repeatedly underwent recurrent *Bathysiphon* crises, after which their taxonomic diversity was restored. These repeated recoveries demonstrate the resilience of the benthic ecosystem during this time. In contrast, the Kotsakhurian *Saccammina* crisis marks the point at which this recovery mechanism was interrupted. Following this event, the former agglutinated assemblages were no longer reestablished, thereby indicating a fundamental reorganisation of the basin ecosystem. The widespread occurrence of monospecific *Saccammina* assemblages, along with their spatial separation from the classical Kotsakhurian brackish-water mollusk assemblages, suggests that environmental conditions across the Eastern Paratethys during the Kotsakhurian were more complex than those expected for a uniformly brackish-water basin. Marine and brackish-water environments likely coexisted in different parts of the basin under contrasting local environmental conditions.

The successive reorganisation of benthic assemblages reflects progressive changes in bottom-water environmental conditions throughout the evolution of the basin. During the Late Kerleutian–Sakaraulian, benthic assemblages were primarily controlled by changes in hydrodynamic activity, which regulated bottom-water oxygenation and organic-matter supply under bathyal conditions. The Kotsakhurian represents the interval of maximum environmental stress, whereas the Tarkhanian records the establishment of the most favourable benthic conditions following basin shallowing and increased marine connectivity.

The Tarkhanian foraminiferal reorganisation represents the second calcareous inversion, but differs fundamentally from the preceding late Sakaraulian inversion. Despite their similar taxonomic expression, the two inversions reflect different evolutionary mechanisms: the late Sakaraulian inversion records local ecological reorganisation within the existing bathyal basin, whereas the Tarkhanian inversion resulted from basin shallowing toward outer sublittoral settings, increased marine connectivity, and faunal renewal. Importantly, this ecological transformation took place while the characteristic Maikop-type sedimentation was still maintained in the Kerch Peninsula sector.

The benthic foraminiferal succession demonstrates that paleoenvironmental reorganisations in the Maikop Basin operated at both local and regional spatial scales. During the Late Kerleutian, Caucasian, and Sakaraulian, benthic assemblage reorganisations were driven by local environmental changes within the Kerch Peninsula sector. In contrast, the Kotsakhurian and Tarkhanian correspond to regional paleoenvironmental events recognised across much of the Eastern Paratethys, indicating large-scale environmental changes that produced broadly similar ecological responses in benthic assemblages. Both local and regional environmental reorganisations were consistently accompanied by ecological crises followed by benthic assemblage reorganisation.

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