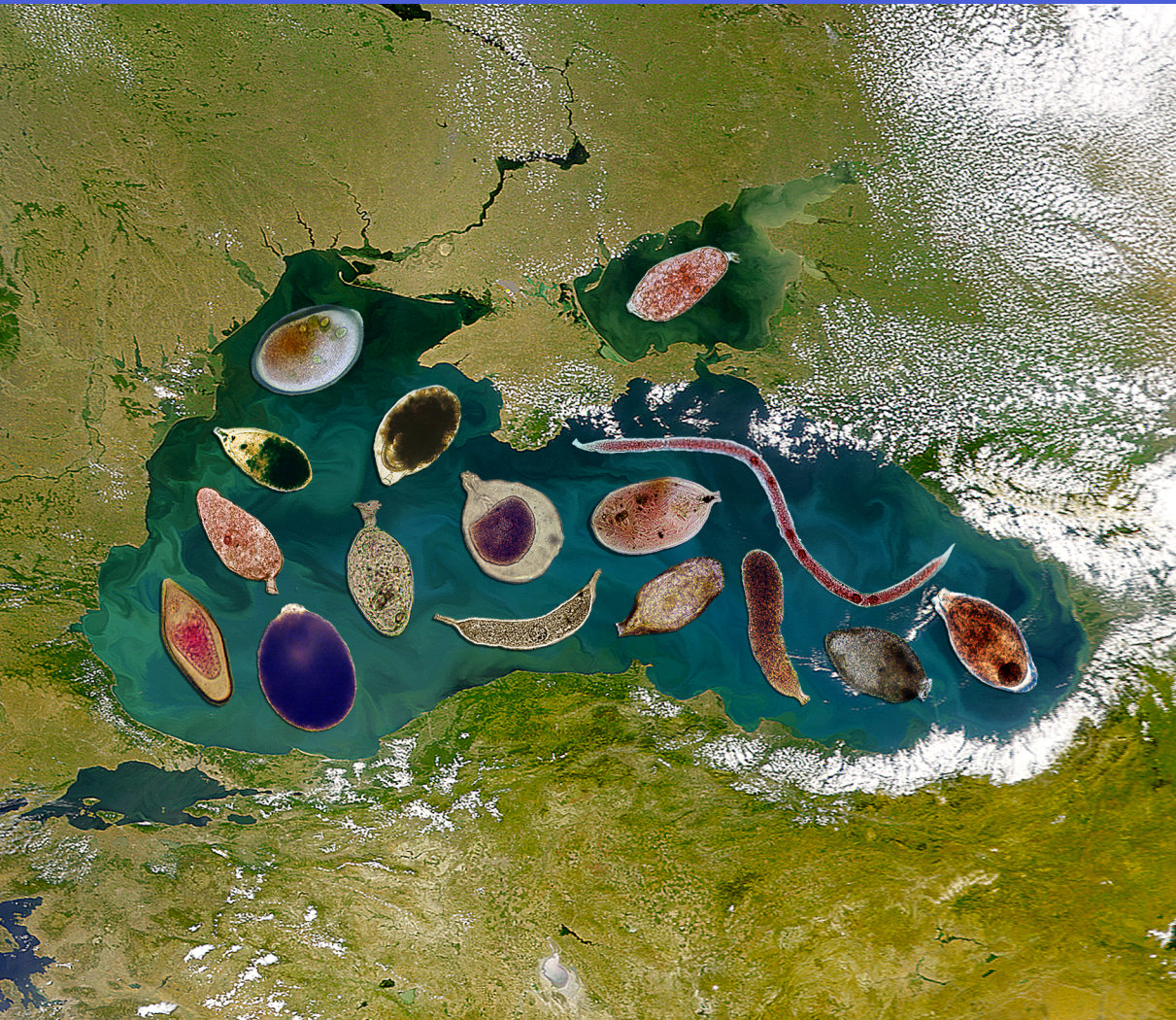


Soft-walled Foraminifera and the Gromiids of the Black Sea and the Sea of Azov: Aspects of Taxonomical Diversity and Ecology

Nelli G. Sergeeva, Oksana V. Anikeeva



**SOFT-WALLED FORAMINIFERA AND THE
GROMIIDS OF THE BLACK SEA
AND THE SEA OF AZOV:
ASPECTS OF TAXONOMICAL DIVERSITY
AND ECOLOGY**

**Nelli G. Sergeeva
Oksana V. Anikeeva**



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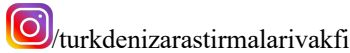
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SUMMARY

This monograph summarizes information on two poorly studied groups of benthic protozoans in the Black Sea and the Sea of Azov - soft-walled foraminifera and gromiids. These protozoans possess delicate proteinaceous tests that are unlikely to fossilize and therefore not of interest to micropalaeontologists and geologists. This limits their utility for studying ancient faunas and their evolution and for addressing important issues in paleogeography. All information about the taxonomy, ecology, and biogeography of these protozoans is based on the study of modern forms. However, benthic protozoans, including soft-walled foraminifera and gromiids, are often not considered by researchers working on benthic communities for various reasons. As our long-term studies of the meiobenthos of the Black Sea and the Sea of Azov have shown, these protozoans are very diverse, numerous, with a wide geographical and bathymetric distribution and form an important component of benthic communities under normoxia and hypoxia/anoxia. The main objective of this monographic work is to acquaint the reader with the soft-walled foraminifera and gromiids of the Sea of Azov and Black Sea, to demonstrate their diversity illustrated with images, and to provide brief diagnoses of the valid species as well as those morphotypes that require further study. A summary of information about the taxonomic diversity of soft-walled foraminifers and gromiids is presented, together with a quantitative evaluation of their contribution to meiobenthic communities along a depth gradient across the mixing zone of oxygen and hydrogen sulfide water masses, down to a depth of 300 m, and in closed bays subject to various anthropogenic impacts. We hope this publication will raise awareness of these protozoans among scientists working on benthic ecosystems in the Sea of Azov and Black Sea, as well as elsewhere.

The monograph is intended for a wide range of specialists, including university professors and their students, in the fields of biology, systematics, ecology, environmental protection.

РЕЗЮМЕ

В монографии обобщена информация о двух малоизученных группах бентосных простейших Черного и Азовского морей - мягкораковинных фораминиферах и громиидах. Эти простейшие обладают нежными органическими оболочками (раковинами), которые не оставляют палеонтологических следов (окаменелостей), в связи с чем не представляют интереса для микропалеонтологов и геологов. Это ограничивает их полезность для изучения древних фаун и их эволюции, а также для решения важных вопросов палеогеографии. Вся информация о таксономии, экологии и биогеографии этих простейших основана на изучении современных форм. Однако бентосные простейшие, включая мягкораковинных фораминифер и громиид, по разным причинам часто не рассматриваются исследователями, изучающими бентосные сообщества. Как показали наши многолетние исследования мейобентоса Черного и Азовского морей, эти одноклеточные очень разнообразны, многочисленны, имеют широкое географическое и батиметрическое распространение и являются важным компонентом бентосных сообществ в условиях нормоксии и гипоксии/аноксии. Основная цель данной монографии – познакомить читателя с мягкораковинными фораминиферами и громиидами Азовского и Черного морей, продемонстрировать их разнообразие и дать краткие диагнозы валидных видов, а также тех морфотипов, которые требуют дальнейшего изучения. В работе представлена краткая информация о таксономическом разнообразии двух вышеуказанных групп простейших, а также количественная оценка их вклада в мейобентосные сообщества по градиенту глубины через зону смешения кислородных и сероводородных водных масс до глубины 300 м и в закрытых бухтах, подверженных различным антропогенным воздействиям. Мы надеемся, что эта публикация повысит осведомленность о данных простейших среди ученых, занимающихся изучением бентосных экосистем Азовского и Черного морей, а также в других регионах.

Монография предназначена для широкого круга специалистов, включая преподавателей университетов и студентов, в области биологии, систематики, экологии и охраны окружающей среды.

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PREFACE

This book, prepared by Dr. Sci Nelli G. Sergeeva and research scientist Oksana V. Anikeeva, provides comprehensive information on the current state of the Monothalamous Foraminifera and Gromiida inhabiting the Black Sea and the Sea of Azov. These benthic protozoans are not well known in the Black Sea basin and therefore, this book fills the gap in scientific research. In addition, this book serves as a reference point to scientists studying both meiobenthos and macrobenthos in the Black Sea. The fact that both soft-walled Foraminifera and Gromiids are part of the food chain at normoxic-hypoxic shallow bottoms and also deep zones up to 300 meters adds to the significance of this book.

I am more than confident that this book is very necessary to better understand this semi-closed sea. I strongly advise this book to all specialists, university professors and their students in the fields of biology and ecology, environmental scientists and nature lovers.

I congratulate both of the authors wholeheartedly for their excellent study of the taxonomy, ecology, and biogeography of these protozoans. On behalf of the Turkish Marine Research Foundation, i am honoured to publish this precious and outstanding book.

April 3, 2024
Beykoz, Istanbul, Türkiye

Prof. Dr. Bayram Öztürk
Head of the Turkish Marine Research Foundation

INTRODUCTION

Marine biologists distinguish three groups of benthic organisms (macro-, meio- and microbenthos – depending on their size) that play specific roles in the functioning of benthic ecosystems. According to the classification developed by Mare (1942), organisms larger than 1 mm are classified as macrobenthos, microscopic organisms 0.1-1.0 mm are classified as meiobenthos and those smaller than 0.1 mm are classified as microbenthos.

The use of this approach to identify ecologically relevant size categories in benthic communities is currently the subject of debate due to the need to consider taxonomic criteria. A detailed analysis of opinions on the independence of these groups and their biological characteristics is contained in the monograph by V.O. Mokievsky (2009, p. 35), who rightly noted that the applied criteria (taxonomic, dimensional) "do not allow to draw an unambiguous border between macro- and meiobenthos." We also came to a similar conclusion regarding the size-related boundaries of meio- and microbenthos. In some cases, we observe that the boundaries between micro-, meio- and macrobenthos unclear (Sergeeva and Anikeeva, this work).

We consider that meiobenthic communities of the Black Sea and the Sea of Azov constitute a unified system of unicellular and multicellular organisms. Among the former, we include protozoans (ciliates, soft-walled and hard-shelled foraminifera and gromiids). Our data show that some representatives of these unicellular organisms exceed the size typical not only for the meiobenthos, but also for the macrobenthos, and play a significant role in the functioning of bottom ecosystems.

In many works (Higgins and Thiel, 1988; Giere, 2009; Maksimov and Petukhov 2011; Sergeeva et al., 2012, 2014, 2015, 2017; Ürkmez et al., 2017) it is noted, that the size of multicellular and unicellular representatives of the benthic fauna occupy the size range 63 μm to 2 mm. In other publications, meiobenthos is considered to only include multicellular organisms, while some authors also include those that are unicellular, but only hard-shelled foraminifera (Vorobyova, 1999; Galtsova, 1991; Mokievsky, 2009; Miljutin et al., 2012). Nevertheless, there is a tendency to emphasize the multicellular component in studying the structure and functional organization of meiobenthic communities.

The vast majority of literature on the diversity, ecology, geographical distribution of allogromiids and gromiids is based on studying the morphology of modern forms. This requires special approaches. Limited knowledge of the morphology and taxonomic diversity, biology, ecology and the role of soft-walled foraminifera and gromiids in organic-matter cycling in marine ecosystems explains why many researchers studying marine benthic communities do not recognize them as organisms.

This review is based on published and original data concerning the diversity and distribution of Foraminifera, Gromiidea, Ciliophora and their contribution to meiobenthic communities of the Black Sea and the Sea of Azov. Our long-term studies of the meiobenthos in these regions have yielded extensive information on the spatial and bathymetric distribution of representatives of these benthic protozoan taxa and their contribution to the structure of benthic communities (Anikeeva et al., 2013; Gooday et al., 2011; Sergeeva and Anikeeva, 2006, 2008; Sergeeva and Dovgal, 2014, 2016; Sergeeva et al., 2012, 2017; Zaika and Sergeeva, 2009). Our own data indicates that they are an important component of meiobenthic communities, accounting for a significant proportion of the total benthic fauna. Soft-walled foraminifera and

gromiids, in particular, are numerous and widespread in these water bodies, from the coastal areas (with normoxic conditions) to a depth of 300 m (hypoxic and anoxic conditions related to the presence of hydrogen sulfide) (Sergeeva et al., 2012, 2015; Sergeeva and Mazlumyan, 2015). These and other unicellular eukaryotes are very diverse, numerous, and play a significant role in the cycle of substances in the bottom ecosystems of the Black Sea and the Sea of Azov (Sergeeva, 2016; Sergeeva and Anikeeva, 2014; Sergeeva et al., 2015, 2017). They constitute a trophic link between bacterial and algal production and higher trophic levels. From literature sources and our own observations, it is known that they are omnivorous, feeding on small bacteria, algae, pollen of terrestrial vegetation, hyphae and conidia of marine filamentous fungi, other protozoan and multicellular invertebrates. In turn, they serve as an important food source for fungi and many benthic invertebrates in a variety of habitats. Our direct microscopic observations have also shown that the cytoplasm of some gromiid species is completely filled with phytosymbionts.

One of our main objectives is to give an overview of the taxonomic diversity of these groups of benthic Protozoa. It is important to note that they have little fossilization potential because they live either as naked cells (e.g., ciliates) or have tests composed of thin, flexible proteinaceous material rather than the rigid test structures composed of calcite or agglutinated particles, characteristic of hard-shelled foraminifera. The test surface in some species of soft-walled protozoans may be agglutinated with minute particles of debris or minerals to varying degrees. At the same time, there are species that accumulate mineral particles and numerous diatom frustules (often of the same species) in the cytoplasm during their life cycle. Gromiids have a thin, transparent, proteinaceous test, sometimes slightly encrusted with sand grains and phytosymbionts, and containing sediment particles and residues of food objects (diatoms, pollen, fungi, crustaceans, etc.).

The aim of this publication is to make information about these little-known groups of benthic protozoans and their role in bottom communities more accessible to specialists studying benthic ecosystems. Descriptions of the morphology and determination of the systematic status of representatives of these protozoan groups are contained in publications that are often difficult for researchers to access. The book therefore summarises the authors' own research and other recent publications on the taxonomic composition, diversity and ecology of soft-walled foraminifera and gromiids of the Black Sea and the Sea of Azov. Information is presented on their distribution along a depth gradient in areas of the open sea, in particular, along the mixing zone of oxygenated and sulfidic water masses to a depth of 300 m in different areas of the Black Sea, as well as in enclosed bays subject to different anthropogenic pressures. Variability in the contribution of these and other protozoans, namely, hard-shelled foraminifera and free-living ciliates, to meiobenthic communities in some bays and zones of the open sea is reviewed in order to assess their role in benthic ecosystems.

The results of analyses of the spatial and bathymetric distribution of foraminifera and gromiids as a component of meiobenthic communities are presented in the series of publications (Sergeeva et al., 2012, 2017; Sergeeva and Gulin, 2007; Sergeeva and Mazlumyan, 2015; Sergeeva and Ürkmez, 2017; Ürkmez et al., 2017) and discussed in Chapter 7-9.

The authors are deeply grateful to Professors A.J. Gooday (England) and J. Pawlowski (Switzerland), academician, Prof. V. Golemansky (Bulgaria), Dr. Derya Ürkmez (Türkiye) for collaborative research on allogromiids, conversations, discussions and publications. The authors are especially thankful to Professor Andrew J. Gooday for editing of our English text. We are grateful to Prof. Antje Boetius (Germany) for the invitation to work within the EU projects HERMES and HYPOX, and the opportunity of collection of materials in scientific expeditions 72/2 R/V 'Meteor', 15/1 R/V 'Maria S. Merian'. We very thanks of Prof. M.N. Çağatay (Türkiye) for the opportunity to participate to our colleagues in the cruise of the RV 'Arar' and to all foreign colleagues - participants in these projects - for their help in obtaining the most interesting materials on the meiobenthos of the Black Sea and further fruitful cooperation.

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List of abbreviations

Mb – Meiobenthos

Gr – Gromia

SWF – Soft-walled Foraminifera

HSF – Hard-shelled Foraminifera

CL – Ciliophora

Coefficient *C* – test's length / width ratio

CHAPTER 1

BENTHIC MONOTHALAMOUS FORAMINIFERA

Soft-walled monothalamous foraminifera have been known for more than 150 years (e.g., Rhumbler, 1903) although their diversity and importance in marine benthic ecosystems has been appreciated only recently (Pawlowski et al., 2013). Numerous investigations in shallow-water and deep-water settings in different parts of the world indicate the high abundance and diversity, particularly of so-called 'soft-walled' types (Altin et al., 2009, Goldstein et al., 2010, Gooday et al., 2011, Majewski et al., 2005, Pawlowski and Majewski 2011, Sergeeva, 2016, Sergeeva and Anikeeva, 2018, Sergeeva et al., 2012, 2013, 2015; Sinniger et al., 2008, Voltski et al., 2014). However, the systematics of soft-walled monothalamous foraminifera is still at an early stage of development in comparison with the hard-shelled, mainly multichambered forms. A purely molecular approach, which has revealed high levels of monothalamid diversity, provides no morphological information about organisms living in a particular environment, which would make the diversity more 'tangible' and available to taxonomic databases. This is especially important in the case of taxonomic groups of which the vast proportion of species are undescribed. Such groups include monothalamids, whose ecology and evolution are also extremely poorly studied (Voltski and Pawlowski, 2015).

Foraminifera include both hard-shelled forms, many of which are multichambered ('polythalamous') and soft-walled forms, all of which are monothalamids. The soft-walled forms have test walls that are composed either of purely of organic material (Order Allogromiida) or of organic material overlain the finely agglutinated particles (Order Astrorhizida, families Saccamminidae and Psammosphaeridae). The soft-walled forms have a very poor fossil record and are often disregarded by micropaleontologists working on modern faunas because they are of no value in palaeoceanographic studies. As a result, there is very little direct information about their evolutionary history. All information about the taxonomic diversity, ecology, and geographical distribution of these Protozoa is therefore based on modern forms.

Among benthic Protozoa, foraminifera are one of the most highly organized groups. They are characterized by the complexity of the life cycle, which can be traced in both modern and fossil foraminifera, the diversity and complexity of the test structure and the sophistication of the pseudipodial system. In developing a system for identifying foraminifera based on morphology, characteristics such as the presence of a proteinaceous, calcareous or agglutinated shell were taken as the basis for the major taxa. Foraminifera with a basically proteinaceous test are termed soft-walled monothalamous foraminifera.

Despite extensive studies of modern and fossil foraminifera, there has been little consensus among taxonomists about their rank in the zoological system. Some authors (Loeblich and Tappan, 1992; Lee et al., 2000) define the status of foraminifera in the zoological system at the Class level. Foraminifera were previously classified as an Order within the subclass Rhizopoda (Mikhalevich, 1968). They are now more commonly regarded as a higher-level group within the supergroup Rhizaria (Adl et al., 2019). The situation is similar, if not more problematic, in the taxonomy of soft-walled foraminifera. It is complicated by the fact that relatively few of the forms recognized can be identified to species level.

Radziejewska et al. (2006) group many of them together despite significant differences between them.

Unlike hard-shelled forms, fossils of soft-walled foraminifera are very rare. It is thought that the ancestors of all other foraminifera should be searched for among the monothalamids (Cushman, 1928; Pawlowski et al., 2003). It is possible that some early foraminifera had mineral-rich cytoplasm, as do members of the modern genus *Psammophaga* (Pawlowski and Maejewski, 2011), and may have thrived in oxygen-deficient environments (Bernhard et al., 2006), leaving fossil remains.

Insufficient knowledge of the species diversity of this group of organisms, not only in the Black Sea but also in other seas and oceans, explains some of the difficulties in developing a taxonomic system for soft-walled foraminifera. The classification of these protozoans based on morpho-anatomical characters (Loeblich and Tappan, 1988) is widely used by researchers. However, in recent years, in addition to classifications based on morphological characters, molecular genetics has been used in order to clarify the relationships between forms from different geographic zones (Gooday and Pawlowski, 2004a; Gooday et al., 2011; Pawlowski, 2000; Pawlowski et al., 1994, 2002). The use of these methods has allowed some species to be revised and their systematic status adjusted (Pawlowski et al., 1999). Among other things, genetic studies have established that the composition of the test wall (either organic or agglutinated) in monothalamids has no phylogenetic significance and cannot be used as a basis for their higher-level classification (Pawlowski et al., 2013). However, genetic analyses are still fairly limited and require specialized expertise. As a result, many studies of the species diversity of soft-walled foraminifera in various marine settings, the description of new species, and their placement within a taxonomic system, have been based on the analysis of morpho-anatomical characters (Loeblich and Tappan, 1988; Gooday and Fernando, 1992; Gooday, Anikeeva and Sergeeva, 2006; Golemansky, 1999 a, b; Sergeeva, Anikeeva and Gooday, 2005; Sergeeva and Anikeeva, 2008, 2018, 2020, 2021).

1.1. The history of study and the current state of the systematics of soft-walled foraminifera

In writing this chapter, we referred mainly to the review article by A. Gooday (2002), which describes the history of soft-walled foraminifera in the most detail.

Until the second half of the last century, soft-walled foraminifera were not mentioned in studies of meiobenthos. However, the study of soft-walled (monothalamous) foraminifera with an organic test began much earlier, in the middle of the 19th century (Holzmann et al., 2021). Until the middle of the 20th century, information about marine soft-walled foraminifera in the literature was fragmentary and, basically, consisted of either brief records of unknown organisms, or were devoted to the description of new species (Siddall, 1880; Lankester, 1903; Rhumbler, 1903; Doflein, 1909; Jepps, 1926; Cushman, 1928). Since the 1940s, studies of these organisms have not only adopted a more systematic (i.e. ordered, regular) character but have also taken certain directions, one of which has been the study of the biology of individual species of soft-walled foraminifera. For instance, the life cycles of *Hippocrepinella alba* Heron-Allen et Earland, 1932 and *Nemogullmia longeverabilis*

Nyholm, 1953 were described in a series of works (Nyholm, 1956; Nyholm and Nyholm, 1975), and their behavior was studied in experiments with live specimens. Works of other scientists (Moodley, 1990; Nyholm and Gertz, 1973; Arnold, 1955; Dahlgren, 1964, Grell 1988) present results of studies on feeding, reproduction and adaptive capacity of individual representatives of this group of organisms. The large naked freshwater species *Reticulomyxa filosa*, which is easily cultured, has been an important laboratory organism in studies of cell motility (Travis and Bowser, 1991)

Although soft-walled foraminifera are widespread in the seas and oceans, from the upper sublittoral to the abyssal depths, and have been studied for over a century, they remain poorly understood. According to the world database WoRMS, the taxonomic list of soft-walled foraminifera includes 555 species (family Allogromiidae - 107 species from 4 genera, 3 subfamilies; family Saccamminidae - 448 species from 61 genera and 2 subfamilies). However, many works on this group of protozoans indicate a large number of undescribed morphospecies (defined only to genus) and morphotypes (defined only to family), reflecting an insufficient knowledge of the systematics of soft-walled foraminifera.

The paucity of data on soft-walled foraminifera as a component of benthic communities partly reflects their similarity to other biogenic structures found in bottom sediments (Gooday, 2002). Researchers sometimes mistake them, at best, for other meiofauna organisms, or ignore them altogether because they don't know what they are. For example, the species *Allogromia marina* Nyholm & Gertz, 1973, in which the cytoplasm is filled with brown stercomata, is rather difficult to distinguish from fecal balls (Nyholm and Gertz, 1973), but other investigations showed that it was gromiid species (Holzmann et al., 2021). The thread-like allogromiids (*Nemogullmia*, *Shepherdella*) are rather similar to nematodes. At the same time, turbellarians can also be mistaken for monothalamous foraminifers, although they differ not only in the presence of internal organs but also, in most cases, in their ciliated surface (Gooday, 2002). The authors of this book have repeatedly encountered this situation themselves while analyzing benthic sediments.

Soft-walled foraminifera are widely reported from many marine habitats. They are recorded in the Pacific (Arnold, 1982), Atlantic (Thalman and Bermudez, 1954; Gooday, 1990) and Indian (Gooday and Fernando, 1992) oceans, in the Mediterranean (Nyholm, 1951), Caspian (Mayer, 1972; Sergeeva and Vodovsky, 2018), Tasman (New Zealand) (Hedley, 1962) seas, off the coast of Sweden (Dahlgren, 1962; Nyholm, 1952, 1954, 1955a,b, 1974), the Sea of Japan (Sergeeva and Anikeeva, unpublished data) and Antarctica (Gooday and Pawlowski, 2004a; Gooday et al., 2004b; Cedhagen et al., 2009).

Numerous populations of allogromiids characterize some brackish estuaries. Two species from the genus *Vellaria* - *V. pellucida* Gooday & Fernando, 1992 and *V. sacculus* Gooday & Fernando, 1992 – were described from the Vellar estuary in Indian (Gooday and Fernando, 1992), and *Allogromia crystallifera* Dahlgren, 1962 is the dominant species in the estuary of the Geta River (Sweden) (Cato et al., 1980). A high number of soft-walled foraminifera was also observed in the Gironde estuary in southwestern France (Soetart et al., 1995). In the estuary of the Ob River (in the inner part) in western Siberia, at a salinity of 20-25‰, allogromiids reached 63-93% of the entire foraminiferal fauna (Korsun, 1999). In many Arctic zones and in the estuary of the Ob River, species of the genus *Psammophaga* dominated. Studies of bottom

samples from the deep part of the White Sea (Mokievsky et al., 2009) revealed that foraminifers as a whole comprised more than 50%, and allogromiids 26%, of total the meiobenthos.

The literature contains scant information on the vertical distribution of soft-walled foraminifera in bottom sediments. According to Goldstein et al., (1995), allogromiids inhabit predominantly the upper sediment layer (0-1 cm) in a saline marsh in Georgia, USA. Some monothalamous agglutinating foraminifera (*Cribrothalammina alba* Heron-Allen & Earland, 1932, *Ovammmina opaca* Dahlgren, 1962, *Saccammina* sp.) also inhabit the sediment surface, although live individuals of another species, *Pseudothurammmina limnetis* Scott & Mediolli, 1980, were found well below the sediment surface in the same salt marsh. Nyholm (1957) observed that *Micrometula* places its elongated body vertically with the aperture directed into sediment. Representatives of the genera *Shepherdella*, *Phainogullmia* and *Nemogullmia* keep their tests horizontal to the surface of bottom sediments. The species belonging to the above three taxa have two apertures located at opposite ends of the elongated test.

In the deep-water part of the White Sea (270 m depth), a difference in the stratification of calcified, agglutinated, and soft-walled foraminifera was observed. Overall, 50% of foraminifers preferred the upper 1 cm layer. Allogromiids are mostly found in the upper two centimeters, but also inhabit the sediment profile to a depth of 5 cm. A similar vertical distribution of allogromiids was observed at all the stations studied (Mokievsky et al., 2009). On the shelf of the Sea of Japan (depths 1-86 m), allogromiids are numerous and widely distributed in various biotopes (own unpublished data).

A.J. Gooday (1986a), studying the stratification of foraminifers in bottom sediments of the bathyal zone (1345 m) in northwestern Ireland, noted a peculiarity in the distribution of recorded species in the bottom sediment at this depth. Thus, allogromiids inhabit the top 4-5 cm of sediment, but 72% of the populations are concentrated in the 0-1 cm horizon, and 15% in the 1-2 cm layer. The species *Nodellum membranacea* (Brady, 1879) is most abundant in the 4-5 cm horizon, while another (not identified) species inhabits only the 2-4 cm layer. At a shallow Antarctic site, Gooday et al., (1996) found species with rounded or oval tests (*Gloiogullmia*, *Allogromia*) concentrated in the upper two centimeters of the sediment, while very elongated or filamentous morphotypes (*Cylindrogullmia*, *Nemogullmia*, *Micrometula*) were distributed in deeper layers.

Observations on the behavior of foraminifera during a long experiment (56 days) showed that some monothalamous foraminifera are able to move in the sediment column to find more favorable conditions (Moodley et al., 1998). At the same time, soft-walled forms (*Allogromia*, *Cribrothalammina*) throughout the experiment showed a tendency to migrate upwards from deeper sediment horizons to the shallower, more oxygenated layers (0 - 0.5 cm). The results obtained testify to the oxyphilicity of these forms.

Soft-walled monothalamous foraminifers are an important component of the foraminiferal communities in the abyssal and bathyal North Atlantic (Gooday, 1986a, b, 1996; Gooday et al., 1998). They are also significant members of the benthic community in the central Arctic Ocean (Schewe and Soltwedel, 1998) and in the oxidative zone bordering the oxygen minimum layer in the northwestern Arabian Sea.

It has been noted (Jumars and Hessler, 1976) that allogromiids are particularly abundant at a depth of 7298 m in the Aleutian Trench. According to A. Sabbatini et al. (2002), soft-walled foraminifers occur in the Atacama Trench (southeastern Pacific) at a depth of 7800 m.

Adaptations of allogromiids to hypoxic conditions are poorly known, and the results of studies on this topic are rather contradictory. For example, their lower representation, in comparison with calcareous forms in upper bathyal oxygen minimum zones leads some authors to conclude that they have a lower ability to adapt to oxygen deficiency. The generally greater ability of calcareous foraminifera to withstand oxygen starvation is explained by physiological ultrastructural and secretory features of carbonate shells that are acquired during phylogeny (Gooday et al., 2000b). According to the authors, it is likely that most soft-walled foraminifera lack such adaptations. However, this is not true in all cases, as shown by the discovery of a monothalamid with bacterial symbionts in the strongly hypoxic Santa Barbara Basin (Bernhard et al., 2000). The same authors (Gooday et al., 2000b) noted that allogromiids were less diverse and constituted a small fraction (<3%) of the community at 412 m depth of the central oxygen minimum zone (OMZ) than at 3340 m depth (35%) – below the OMZ.

In the Santa Barbara Basin, where oxygen concentrations are less than 0.05 mL x l⁻¹, soft-walled foraminifera account for 1.4% of the foraminiferal community (Gooday et al., 2000a). These data are consistent with the results of a microcosm experiment (Moodley et al., 1998) in which, on average, 17% of the soft-walled foraminiferal abundance remained in the oxygen-free sediment layer by the end of the 56-day experiment compared with 33% of calcareous foraminifera, of which *Nonionella turgida* Williamson, 1858 represented more than half. The results of earlier experiments (Moodley et al., 1997) also suggest that calcareous and other hard-shelled foraminifera are more tolerant to anoxic conditions than soft-walled forms.

In contrast to the evidence for reduced tolerance to low-oxygen conditions among monothalamids, there was no clear decrease in the relative or absolute abundance and biomass of this group during the natural dysoxia (anoxia) in Gulmar Fjord (west coast of Sweden) during the winter of 1979-1980 and later years (Josefson and Widbom, 1988). It has also been noted (Nyholm, 1956) that some allogromiids (*Cylindrogullmia alba* Nyholm, 1974, *Gloiogullmia eurystoma* Nyholm, 1974, *Nemogullmia longevariabilis*) "live under extreme oxygen deficit" in the same region. Bernhard (1996) points to a connection between *Allogromia* sp. and filaments of the large sulfide-oxidizing bacterium *Beggiatoa*, which lives in the redox zone. These studies indicate that some organic-walled species are more resistant to oxygen deprivation.

Some soft-walled foraminifera species inhabit empty calcareous and agglutinated foraminiferal shells (Moodley, 1990). At first glance, they look like ordinary multichambered foraminifers. The SWF occupies only the last chamber of the hard shell. The main advantage of this way of life is the acquisition of a solid protective shell at low energy costs. During the experiment, it was found that not all soft-walled foraminifers preferred to seek refuge in the empty shells of their hard-shelled relatives. Instead, some agglutinated quartz grains to their organic test, thereby giving it greater strength. This preference depends on the size and elasticity of the soft-walled forms. A. Gooday (1986b) found in bottom sediments samples taken at a

depth of 1330 m southwest of Ireland, from 2.2% to 12.2% of all SWF occupied empty planktonic foraminiferal shells.

Information about the selective capacity of soft-walled foraminifera in the genus *Psammophaga* Arnold, 1982 to accumulate specific mineral particles (magnetite, titanomagnetite, and zircon) in the cytoplasm was published during the past decade. Two new species were described, based on this characteristic. The cytoplasm of *Psammophaga magnetica*, from shallow-water sediments in West Antarctica, contains magnetite and titanomagnetite crystals (Pawlowski and Majewski, 2011), and *P. zirconia* from the central Adriatic Sea accumulates intracellular zircon (51%) and titanium minerals (27%) (Sabbatini et al., 2016). Pawlowski and Majewski (2011) also transferred *Allogromia crystallifera* Dahlgren, 1962 to the genus *Psammophaga*, based on the presence of mineral particles distributed more or less uniformly throughout its cytoplasm. Sabbatini et al. (2016) suggest that there is a species-specific selectivity for certain minerals among different species of this genus. This apparent selective ability makes species such as *Psammophaga* cf. *crystallifera*, *P. zirconia* and *P. magnetica* attractive for studying the interaction of these foraminifera with the environment. The most likely hypothesis explaining the ability of *Psammophaga* species to select and concentrate zircon and other heavy minerals is that this is an advantage for maintaining the stability of the organism in the sediment enabling it to feed more efficiently.

Together with discussions about the distribution of certain SWF species identified only on the basis of morphological characters, interest in genetic studies of this group protozoans has recently increased (Pawlowski et al., 2002, 2003; Voltski and Pawlowski, 2015; Habura et al., 2008; Cedhagen et al., 2009; Gschwend et al., 2016; Holzmann et al., 2021; Gooday et al., 2022). The first molecular data relating to the systematics of SWF were published at the end of the last century (Pawlowski et al., 1994).

According to traditional classifications, monothalamous members of the family Saccamminidae differ from members of the family Allogromiidae solely in the presence of an agglutinated test wall (Loeblich and Tappan, 1964; Kaminski, 2014). However, Lipps (1973) believes that such a division may be erroneous. Subsequent morphological, cytological and behavioral studies (Bowser et al., 1995) proved the close relationship between the two groups and raised several questions regarding their taxonomic and phylogenetic affinity. DNA analysis confirmed a close phylogenetic relationship between allogromiids and astrorhizids, nullifying their separation and requiring a complete taxonomic revision of both groups. The grouping of agglutinated and organic-walled monothalamids in the same phylogenetic clades based on genetic data clearly shows that these taxa are artificial (Pawlowski et al., 2013). However, further genetic studies are needed to test the relationship between different groups (including both soft-walled and hard-shelled monothalamids) and assess the importance of shell structure as the main criterion for determining higher taxa of foraminifera (Pawlowski, 2000; Pawlowski et al., 2003).

Thanks to genetic research, it is also possible to identify and correct errors in the taxonomy of soft-walled foraminifera. Thus, *Reticulomyxa filosa* Nauss, 1949, a naked fresh-water 'amoeba' erroneously assigned to the class Granuloreticulosea (freshwater amoeba), took its place among the foraminifera after molecular phylogenetic analysis, (Pawlowski et al., 1999).

Another important direction in the study of soft-walled monothalamous foraminifers is that of the study of the fine structure of the cytoplasm using electron microscopy (Goldstein and Richardson, 2002). In an early study, the existence of microtubules of two types were observed in the cytoplasm of *Cylindrogullmia alba* (Nyholm & Nyholm, 1975), as well as in *Nemogullmia longevariabilis* (Nyholm, 1955b). The maximum length of microtubules is 3 μm . Their position in the cytoplasm is peripheral, they are arranged in layers and interconnected by "bridges". The authors suggest that these inclusions constitute an important part of the cellular cytoskeleton. They also mention its presence in species such as *Allogromia laticollaris*, *P. crystallifera* and *Micrometula hyalostriata*. Foraminiferal microtubules have unique characteristics and are fundamental to the functioning of the reticulopodial system (e.g., Travis and Bowser, 1991; Habura et al., 2005; Hou et al., 2018). They help to capture bacteria from the substrate and transport them (as food) through the aperture into the cell. It is also suggested that elongation of microtubules may be associated with the concentration of Ca^{2+} ions in the cytoplasm.

The ability of some SWF species to accumulate toxic products in the cytoplasm is interesting. This feature was noted in *Toxisarcon synsuicidica*, large, mainly naked (non-testate) foraminifera from the family Astrorhizida *incertae sedis* inhabiting the western coast of Sweden (Cedhagen and Pawlowski, 2002). The accidental "release" of accumulated toxins can harm the organism. Morphological features of *T. synsuicidica* are the large size of the cell, outwardly similar to a "branched" lump of detritus or an accumulation of sediment. Another species of this genus, *Toxisarcon alba*, was described by Wilding (2002) from the west coast of Scotland. It forms a naked cell resembling a giant amoeba.

The systematic position of the new species is defined as follows:
Supergroup Rhizaria Cavalier-Smith, 2002
Phylum Foraminifera d'Orbigny, 1826
Class Monothalamea Haeckel, 1862 (sensu Pawlowski et al., 2013)
Order Allogromiida Loeblich et Tappan, 1961
Order Astrorhizida Brady, 1881

CHAPTER 2 GROMIIDA

2.1. The history of study and the current state of the systematics of the gromiids

Gromiids are amoeboid monothalamous (single-chambered) protozoans, with a proteinaceous test and filamentous pseudopodia. They range in size from 200-300 μm to several centimeters. Currently, they are all assigned to the same genus, *Gromia*. The systematics of *Gromia* has a complicated history. The following brief summary is based on Rothe et al., (2009), where it is presented most fully.

Over the years, ideas about the phylogenetic placement of *Gromia* have changed considerably. Until fairly recently, their classification was based purely on morphological features. An important advance was made by Rhumbler (1903), who recognized that the filose pseudopodia of *Gromia* were different from the granuloreticulose pseudopodia of foraminifera. This criterion enabled Hedley (1958) to clearly differentiate *G. oviformis* from the foraminifera *Allogromia ovoidea* Rhumbler, 1903, with which it had long been confused. The nature of the pseudopodia was the main basis for classifying gromiids within the class Filosea (Hedley, 1962; Ogden & Hedley, 1980; Bovee, 1985). Thus the revised classification of the Protozoa published by Levine et al. (1980) assigned gromiids to the phylum Sarcomastigophora, subphylum Sarcodina, superclass Rhizopoda, class Filosea, order Gromiida. However, this failed to settle the question and two decades later Patterson, Simpson and Rogerson (2000) adopted a more cautious approach and referred to gromiids as ‘amoebae of uncertain affinities’, most likely related to the Foraminifera and testate filose amoebae.

Towards the end of the last century, the first molecular analyses of *Gromia* began to provide more accurate insights into the phylogenetic position of gromiids. Initial results assigned *G. oviformis* to the phylum Rhizopoda at the crown of the ribosomal eukaryotic tree (Pawlowski et al., 1994). A series of later genetic studies, beyond the scope of the present publication, have refined the relationships between gromiids and other protists. In brief, gromiids are now firmly established, together with the foraminifera, as members of the ‘supergroup’ Rhizaria, one of the major subdivisions of the eukaryotic tree of life (e.g. Keeling et al., 2014). However, within the Rhizaria, gromiids and foraminifera are classified in different higher-level groups, most recently either the Endomyxa and Ectoreta (Cavalier-Smith et al., 2018) or the Endomyxa and Retaria (Adl et al., 2019), respectively.

Gromiids and soft-walled foraminifera in the Black Sea (Istanbul Strait (Bosporus), depths 75-300 m) account for a significant proportion of the total number of meiobenthos both in normoxia and acute hypoxia up to the anoxic/hydrogen sulfide zone (Sergeeva et al., 2013; 2017; Sergeeva and Ürkmez 2017). According to our data (Sergeeva and Gulin, 2009), gromiids inhabit bottom sediments enriched with methane seeps in the oxic-anoxic zone of the Dnieper Paleo-Delta. In the shelf zone of the Sea of Japan, gromiids are widespread in the depth range 1-86 m. Our preliminary data suggests that the gromiid fauna in this region includes at least 4-5 species (Sergeeva and Anikeeva, unpublished data).

Research on the Barents Sea gromiids (Gooday et al., 2013) revealed small-sized specimens that range in shape from oval and drop-shaped to sausage-like and more elongated, worm-shaped forms. Some specimens from this region are considerably smaller (<200 μm) than other individuals in this group, which often exceed 1 mm in length (Rothe et al., 2009).

An interesting study on nitrate respiration by *Gromia* and foraminifera was carried out by Piña-Ochoa et al. (2010). They found that several different groups of foraminifera as well as *Gromia* accumulate nitrate and breathe through denitrification. The contribution of eukaryotes to the removal of fixed nitrogen by respiration, according to the authors, may equal the importance of bacterial denitrification in oceanic sediments.

The genus *Gromia* Dujardin, 1835 includes benthic protozoans, some of which are quite large (specimens of at least one species may be larger than 1 cm) inhabiting shallow to deep waters. On the basis of general morphology, *Gromia* was considered to be a kind of foraminifera with a similar life cycle. However, members of this genus are distinguished by the absence of anastomosis in the pseudopodia and meiosis of gametes in other stages of the cycle. However, molecular analysis has shown that Foraminifera and Gromiida are separate branches of the Rhizaria (Burki et al., 2002; Rothe et al., 2011; Cavalier-Smith et al., 2018). As well as soft-walled foraminifera, representatives of the genus *Gromia* have been mentioned in works on the Black Sea (Golemansky 1999a, 2007; Sergeeva 2016; Sergeeva et al., 2012, 2013, 2017).

Twenty described species of gromiids are in WoRMS, but this remains a poorly known group taxonomically. However, these relatively large and conspicuous protozoans have been recognised at increasing numbers of marine sites around the world, from intertidal to extreme hadal depths (Arnold, 1972; Matz et al., 2008; Rothe et al. 2009; Sergeeva et al., 2012; 2017; LeDuc and Rowden, 2017; Gooday and Goineau, 2019; Gooday et al., 2021) and they clearly encompass many undescribed species (Aranda da Silva and Gooday, 2009; Gooday et al., 2021; Rothe et al., 2011; Sergeeva and Anikeeva, 2018; Pavel et al., 2021).

According to WoRMS (2023), 20 species of *Gromia* have now been officially described. However, many of the *Gromia* species described in the 19th and early 20th centuries are not gromiids but freshwater foraminifera or other kinds of protozoans (Holzmann et al., 2021). In addition, *Gromia dujardinii* Schultz 1854 is a synonym of *G. oviformis* and *G. dubia* Gruber 1884 is probably as well. According to Prof. Gooday, there are several other *Gromia* species mentioned in WoRMS (solenopus, granulata, appendiculariae) that are *incertae sedis*.

For us, the problematic issue of the taxonomy of this group of protozoa arose when we discovered an unusual specimen, while studying the meiobenthos of the Catherine Grotto of the Black Sea in 2021. This specimen possessed a large number of apertures over the entire test surface (this work, section 6.2).

In the present study, the description of gromiid morphospecies from the Black Sea and the Sea of Azov completes our knowledge of the diversity of these protozoans.

Suprageneric classification follows Bovee, 1985 (Gooday et al., 2000a, 2021; Adl et al., 2019):

Supergroup Rhizaria Cavalier-Smith, 2002.

Class Gromiidea Cavalier-Smith, 2003.

Order Gromiida Claparède & Lachmann, 1856.
Family Gromiidae Reuss, 1862.
Genus *Gromia* Dujardin, 1835

CHAPTER 3 MATERIAL AND METHODS

3.1. Study areas

The review of soft-walled foraminifera and gromiids is based on the literature and own data obtained during 1985-2021. Cooperation with scientists from various countries within the framework of international EU projects (HERMES, HYPOX, CRIMEA, PERSEUS, SCOPES), TUBITAK-NASU (Ukraine-Türkiye) and the implementation of national scientific (Ukrainian and Russian) programmes allowed us to obtain a large volume of material from various regions of the Black Sea, from coastal waters down to a depth of 300 m where oxygen and hydrogen sulfide water masses and normoxic conditions are replaced by acute hypoxia and anoxia. In recent years, our IBSS colleagues have given us collections of bottom sediments from the Sea of Azov and its hypersaline estuary, Sivash, to study meiobenthos and its components.

In order to illustrate the distribution of soft-walled foraminifera and gromiids and their contribution to meiobenthic communities we will consider some examples from a few distinctive areas. The material was collected from bottom sediments obtained in different years in the coastal and deep-water areas of the Black Sea and the Sea of Azov (Fig. 3.1, Table 3.1).

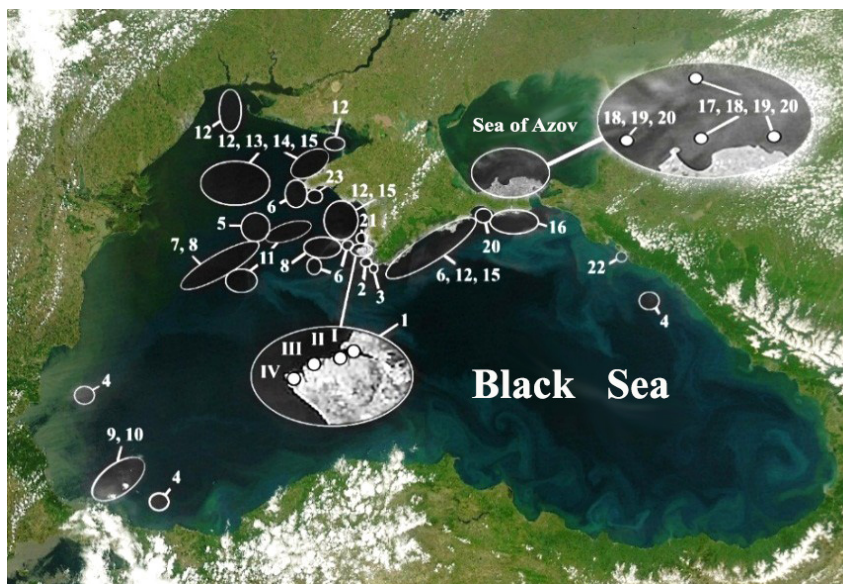


Figure 3.1. Areas and stations where samples for meiobenthic and protozoan research was obtained (by Sergeeva and Anikeeva, 2018)

Table 3.1. Data for areas in the Azov-Black Sea basin where sediment samples were collected for meiobenthos research (MUC – multi-corer, GT – geological corer, PsC – pushcorer, BgO – bottom grab “Ocean-50”, Bg – Petersen bottom grab, Mg – manual grab by diver, Mbt – meiobenthos tube)

№ (Fig.4.1)	R/V, cruise number	Year of collection	Depth, (m)	Number of stations	Research area	Selection method
4	Academik Kovalewsky, 102	1986	20-140	17	Shelves of Bulgaria, Caucasus, Türkiye	BgO
5	Professor Vodyanitsky, 45	1994	76-607	12	NW of the Black Sea	BgO
6	Professor Vodyanitsky, 53	1999	23-260	12	NW of the Black Sea and SE of Crimea	BgO
11	Poseidon, 317/3	10.2004	182-252	8	NW of the Black Sea	MUC
7	Meteor 72/2	03.2007	120-240	11	NW of the Black Sea	MUC, PsC
10	Arar, ITU	09.2009	75-300	9	Istanbul Strait (Bosporus) area	MUC, GT
9	Maria S. Merian, 15/1	04.2010	80-296	13	Istanbul Strait (Bosporus) area	MUC, GT
8	Maria S. Merian, 15/1	05.2010	83-375	25	NW of the Black Sea (Crimea)	MUC, PsC
12	Professor Vodyanitsky, 64	07.2010	30-121	16	NW and E of Crimea shelves, the Sea of Azov	BgO, GT
13	Professor Vodyanitsky, 68	11.2010	19-123	26	NW, W and E of Crimea shelf	BgO
14	Professor Vodyanitsky, 70	08.2011	10-145	32	NW, W and E of Crimea shelf	BgO
15	Professor Vodyanitsky, 72	05.2013	16 -102	41	NW, W and SE of Crimea shelves	BgO
16	Professor Vodyanitsky, 75	07.2013	60-249	16	SE of Crimea shelf	BgO, GT, Mbt
17	Professor Vodyanitsky, 83, 108	01.2016	9-58	13, 5	The Sea of Azov	BgO, Mbt
18-20	Professor Vodyanitsky,	06.2016 10.2016 07.2017	80-11 96-107	21	The Sea of Azov, SE of	BgO, Mbt

	86,90, 96, 100, 106, 108,113	12.2017 2019, 2020			the Black sea shelf	
1 (I, II, III, IV)	Felucca	2001-2017	3-35	>100	Bays of Sevastopol	Bg, Mg, Mbt
3	Samples of SCUBA diver	2017	0-30	22	Laspi bay	Mbt,
2	Samples of SCUBA diver	2005	5-22	17	Underwater channal Balaklava	Mbt
21	Samples of SCUBA diver	2003	1-25	25	Uchkuevka- Lyubimovka	Mg, Mbt
22	Samples of SCUBA diver	2018	1-4	3	NE, Golubaya bay	Mbt
23	Samples of SCUBA diver	2004	2-7	5	Cape Tarkhankut	Mbt
24	«Ashamba»	2019	82-190	10	NE of the Black Sea	BgO
25	Samples of SCUBA diver	2020	0-6	12	NE of the Black Sea	Mg, Mbt
26	Samples of SCUBA diver	2021	0-4	16	Ekaterininsky grotto, Cape Aya	Mg, Mbt

When discussing the spatial and vertical distribution of these groups of protozoans, maps showing the distribution of meiobenthos stations in the corresponding areas will be presented (Chapters 7-9).

3.2. Sampling and processing methods

Samples of bottom sediments for biological studies were collected at the oxic/anoxic interface of the SW and NW parts of the Black Sea using a multiple corer (MuC, $\varnothing = 9.6$ cm), push corer (PsC, $\varnothing = 7.3$ cm) or geological corer (GT $\varnothing = 7.3$ cm) and devices that obtain virtually undisturbed samples. Two or three cores were analyzed at each station from independent MuC or PsC casts. The upper 7-10 cm of each core were sectioned horizontally in one-centimeter intervals. Sampling in oxic zones at the NW of the Black Sea and NW shelf of Crimea was conducted using smaller push cores ($\varnothing = 4$ cm).

In the oxic zone of the Black Sea at open shelf sites off the Crimean Peninsula and in bays around the Peninsula, bottom grabs (Ocean-50) were used to collect sediment samples. In addition, three replicate sediment cores, 5 cm high ($\varnothing = 4.8$ cm), were taken from box cores. All of these samples were fixed separately with 4% formalin or 75° alcohol. Cores 5-10 cm high, obtained with a MUC (core diameter 9.5 cm), GR ($\varnothing 7$ cm) and PsC ($\varnothing 7.3$ cm), were sliced into 1 cm layers, each of which was also fixed separately.

Sediments were washed through 1 mm and 63 μ m sieves and stained with Rose Bengal solution before sorting in water under a microscope for "live" (stained) organisms. The stained sample was placed in a Bogorov chamber and meiofaunal organisms were picked out under an MSP-2 binocular microscope. Samples were sorted by major meiofaunal taxa and counted. We extracted only those specimens that

stained intensely with Rose Bengal and showed no signs of morphological damage. All recovered organisms were counted and identified to the high taxa.

Protozoans were placed in temporary glycerine preparations and examined using MSP-2 microscopes at 30-90x magnification, as well as Olympus CX41, Mikmed-6 and Nikon E-200 microscopes at 100-1000x magnification; all microscopes were equipped with PC-connected cameras for more detailed examination of morphological features. Specimens were measured with QuickPhoto Microprogram, or an ocular micrometer, and identified where possible to genera or species. The large number of specimens that can be identified only to genus were referred to undescribed morphospecies. If they can only be identified to family level, we assigned them to morphotypes.

The density of soft-walled and hard-shelled Foraminifera, Gromiida and Ciliophora, as well as all other components of meiobenthos, was calculated per m² of the bottom. Permanent preparations (glycerin-gelatin) of specimens of described species, undescribed morphospecies and morphotypes from the Black Sea make up the collection of this group in the Institute of Biology of the Southern Seas of the Russian Academy of Sciences (Sevastopol). The identification of these specimens with brief descriptions is the basis for creating an electronic version of the collection.

Our studies have shown that protozoans are an important component of micro-, meio- and even macrobenthic communities of the Black Sea and the Sea of Azov. They are a food source for many benthic invertebrates and form a link between bacterial and algal production and higher trophic levels. At the same time, they also prey upon other protozoans as well as metazoans.

Protozoans from the outlet area of the Istanbul Strait's (Bosporus) into the Black Sea comprise Gromiida, Ciliophora and Foraminifera, in particular the hard-shelled and soft-walled single-chambered (monothalamous) taxa. Gromiidae and large allogromiids (soft-walled foraminifera) may have been disregarded because of their similarity to faecal pellets (Nyholm and Gertz, 1973). For many years, these organisms have been difficult to classify taxonomically or even recognize as protozoans (Gooday et al., 2000b). They are also characterized by a small volume of cytoplasm contained within a large volume of test, making it difficult to establish their biomass. Gromiids and soft-walled foraminifera in the coastal zone of Bulgaria were first noted by A. Valkanov (1970) and V. Golemanski (1974, 1999a, b). Later, these protozoans were found along the shelf and continental slope of the Black Sea in conditions of oxygen deficiency (Sergeeva, 2003; Sergeeva and Gulin, 2007). Gromiids were a constant component of meiobenthos at all depths investigated, representing up to 30% of the assemblage. Ciliates constitute the major proportion (15-90%) at depths of 103, 250, 300 m, while foraminifera constitute the major proportion at depths of 82, 160, 190 m.

Analyses of monothalamous foraminifera, gromiids, and ciliates suggest that the oxic/anoxic transition zone supports abundant and diverse protozoan communities. Together, these results confirm our early conclusion about a possible adaptation of some benthic groups to hypoxia/anoxia and the hydrogen sulfide environment (Sergeeva et al., 2012). Our data suggest that some of these protozoans, as well as some metazoans (hydrozoa, nematodes, and polychaetes) have indeed adapted to live under hypoxic/anoxic and sulfidic conditions in the Black Sea. This fauna is indigenous, rather than having been transported from adjacent oxygenated areas.

CHAPTER 4

THE CURRENT STATE OF STUDY OF THE MONOTHALAMOUS FORAMINIFERA AND GROMIIDS IN THE BLACK SEA AND THE SEA OF AZOV

In 1985-1986 one of the authors of this monograph (N.G. Sergeeva) noticed that small-sized objects of undefined systematic status are often recorded in bottom sediment communities of the Black Sea. According to their size, they were classified as meiobenthos (Mare, 1942). Their numbers and frequency of occurrence were quite considerable and they had a wide spatial and bathymetric distribution across this region. Moreover, morphotypes with distinctive morphological features could be clearly distinguished among individuals from different regions of the Black Sea.

In the book "Introduction to the Study of Meiofauna" (Higgins and Thiel, 1988), the chapter "Foraminifera" (A. Gooday) included two morphological groups, those with hard shells and those with proteinaceous tests, very similar to the organisms we found in the Black Sea. Thanks to this work, we fairly confidently identified the unknown organisms from the Black Sea as soft-walled foraminifera. The identification of specimens of the Black Sea organisms, that we took to the United Kingdom for examination, was confirmed by an expert on this group of foraminifera, Professor A. J. Gooday.

Benthic protozoans, namely Foraminifera, Gromiida and Ciliophora, are widespread and abundant in the Sea of Azov and the Black Sea. Long-term studies of Black Sea meiobenthos have provided extensive information on the diversity, spatial and bathymetric distribution of benthic representatives of these groups and their contribution to the structure of bottom communities (Vorobyeva, 1999; Sergeeva, 2003; Revkov and Sergeeva, 2004; Sergeeva and Gulin, 2007; Sergeeva et al., 2012; Sergeeva and Anikeeva, 2014; Sergeeva and Mazlumyan, 2015; Sergeeva et al., 2017). Protozoans, as well as multicellular organisms, have been found to be an important link in marine benthic communities, and may account for a significant proportion of total benthic faunal abundance. The hard-shelled foraminifera (HSF) of the Black Sea are well studied (Yanko and Troitskaya, 1987; Yanko and Vorobyeva, 1991; Temelkov et al., 2006; Golemansky, 2007). The following chapters examine the quantitative distribution of SWF and HSF in selected areas of the Black Sea and the Sea of Azov along a depth gradient when conditions change from normoxia to hypoxia and anoxia.

The first references to soft-walled foraminifera and gromiids of the Black Sea date from the end of the last century (Sergeeva and Kolesnikova, 1996; Golemansky, 1999a, b). They are distributed across a wide depth range, from the supralittoral to the lower limit of the sublittoral (Anikeeva and Sergeeva, 2001; Sergeeva and Anikeeva, 2006; Gooday et al., 2006; Sergeeva and Anikeeva, 2014; Sergeeva et al., 2005, 2010, 2012, 2015, 2017; Sergeeva and Mazlumyan, 2013, 2015). Our data indicate that some species are confined to certain regions, depths and biotopes of the Black Sea and the Sea of Azov, while others are eurybionts. For example, in the bays and open zones near Sevastopol, the fauna of soft-walled foraminifera is characterized by a distinctive species composition, the dominant role of certain representatives, but also

some variation in faunal densities (Anikeeva, 2003, 2005a, b, 2007; Sergeeva and Anikeeva, 2014; Sergeeva et al., 2015).

The broad bathymetric distribution of soft-walled foraminifers and gromiids in the Black Sea is described in several papers (Sergeeva and Anikeeva, 2018; Sergeeva et al., 2015, 2017), that discuss changes in the density of the coastal and deep-water communities. Soft-walled foraminifera include both eury- and stenobiotic species. The concentration of oxygen in the environment regulates the distribution of soft-walled as well as other foraminifera.

Research on the Black Sea meiobenthos in recent decades has shown that soft-walled foraminifers and gromiids are an important component of benthic communities in this region. For example, the proportion of benthic protozoans (foraminifera, gromiids and ciliates) in the meiobenthos as a whole varied from 6 to 12% along a depth gradient (80-300 m) in the north-western area of the Crimea and offshore Türkiye (Istanbul Strait (Bosphorus)'s area). The contribution of soft-walled foraminifera to the benthic protozoan assemblage ranged from 12 to 60% (Sergeeva et al., 2017).

In the northwestern part of the Black Sea, soft-walled foraminifera of the families Allogromiidae and Saccamminidae are more abundant at depths of 130-260 m under hypoxic and anoxic conditions compared to hard-shelled calcareous forms (Sergeeva, 2003; Sergeeva and Kolesnikova, 1996). At the same time, they are also a component of specific meiobenthic communities of the Black Sea redox zone.

However, many researchers studying benthic ecosystems ignore soft-walled foraminifera and gromiids in their collections. There are a variety of reasons for this. The primary reason seems to be that protozoans are regarded as a component of the microbenthos rather than the meiobenthos (Mare, 1942). At the same time, insufficient information about these groups of protozoans, together with ignorance of their size and morphological characters, leads to their underestimation as a functional component of benthic communities.

The systematics of soft-walled foraminifera based on morphological features is still incomplete. Therefore, when species are difficult to identify based on morphological characters, the forms represented in collections are often differentiated into separate morphotypes and morphospecies that are easily recognizable in later studies of diversity and ecology (Gooday et al., 2004b; Radziejewska et al., 2006). The same approach has been adopted in our studies (Sergeeva and Anikeeva, 2006; Sergeeva et al., 2010, 2015). In recent years, together with the use of morphological characteristics, genetic data (sequences) have been included in the description of new species, including Black Sea species, and revision of known species, but these works are not numerous (Gooday et al., 2011).

The original summary of soft-walled foraminifera diversity (Sergeeva and Anikeeva, 2006) of the bays of the Sevastopol area included 17 representatives, among which were four valid species: *Tinogullmia lukyanovae* Gooday, Anikeeva & Sergeeva, 2006, *Psammophaga simplora* Arnold, 1982, *Vellaria pellucida* Gooday & Fernando 1992 and *V. sacculus* Gooday & Fernando 1992. The first of these was described as a species new to science, the other three species were recorded for the first time in the Black Sea. The remaining seven representatives remained as morphotypes, the description of which was left for the future. Subsequently, two new genera and species *Nellya rugosa* Gooday, Anikeeva & Pawlowski, 2011 and

Cedhagenia saltata Gooday, Anikeeva & Pawlowski, 2011, were described from the same habitats based on their morphological and genetic characteristics (Gooday et al., 2011). Two new species, *Goodyia rostellata* Sergeeva & Anikeeva, 2008 from open areas of the Black Sea, and *Guanduellia podensis* Temelkov, 2010 from Bulgarian coastal waters, were also described. A new species first discovered in the hypersaline conditions of the Sivash estuary (the Sea of Azov) was described as *Vellaria solenta* (Sergeeva and Anikeeva, 2021).

Our subsequent investigations of deep-sea soft-walled foraminifers of the Black Sea suggested the presence of specific adaptation mechanisms to the extreme conditions of the Azov-Black Sea basin. Variability of the taxonomic diversity and density of soft-walled foraminifers under conditions of normoxia and hypoxia caused by different processes is described for several areas adjacent to Sevastopol (Kruglaya and Sevastopol Bays, the open sea - roadstead). The specific conditions in the study areas are determined by natural (topography, season, depth) and anthropogenic factors (recreation, hypoxia and pollution resulting from human activities). In total, 18 representatives of this group were recorded in the Sevastopol area, 11 of them in Kruglaya Bay, 5 in raid area and 14 in Sevastopol Bay. The abundance of the species varied during the observation period (Sergeeva and Anikeeva, 2014).

A significant diversity of soft-walled foraminifers in the zone of methane gas seeps in the NW part of the Black Sea (depth range 120-240 m) is reported from materials obtained in 2007 during an expedition on the R/V "Meteor" (Germany). Allogromiids present here included two species, *Tinogullmia* cf. *riemanni* Gooday, 1990 and *Goodyia rostellata*, as well as 9 morphospecies and 16 morphotypes. Saccamminids are represented by two morphospecies defined to genus level and 10 as morphotypes. The maximum abundance of foraminifera according to depth was recorded in the range 150-160 m. At 230-240 m depth, 2-10 species, each represented by single specimens, were observed (Sergeeva et al., 2010).

Data on the density and taxonomic composition of soft-walled and hard-shelled foraminifera (Sergeeva et al., 2015) showed a wide spatial distribution of the former with depth, from shallow bays to the permanently sulfidic and anoxia areas of the open sea. The ratio of the abundance of soft-walled monothalamous and hard-shelled foraminifers demonstrates the predominance of monothalamous forms in both shallow shelf waters and deep zones with permanent hypoxia, revealing their greater tolerance to extreme conditions.

The data presented here on the taxonomic composition of soft-walled foraminifers in the Black Sea and the Sea of Azov show that the systematics of this group of organisms and their role in benthic communities is insufficiently studied. However, it is clear that the study of these foraminifers using different approaches remains a priority not only in relation to the Azov-Black Sea fauna, but also other seas and oceans.

Another group of benthic Protozoa, the Ciliophora, is represented in the Black Sea by 476 species (Azovsky and Masey, 2003a, b), all of which are confined to the oxygenated zone. The results of our studies of soft-walled foraminifera in the Black Sea and the Sea of Azov convince us that further detailed studies will undoubtedly yield a level of species diversity comparable to that of the ciliates. In this regard, it should be noted that our list of soft-walled foraminiferal morphotypes of the Black Sea and the Sea of Azov should be considered as preliminary and not limited to the

94 taxa included in the present publication. In particular, our collections include about 20 morphospecies belonging to the genus *Psammophaga* and other allogromiid genera that require further detailed analysis. For this reason, we don't yet include them in the SWF list presented in this work.

A summary of modern soft-walled foraminifers of the Bulgarian coastal zone (Temelkov, Golemansky and Todorov, 2006) includes 6 representatives, two of which are identified only to the genus level. According to our unpublished data, *Psammophaga* cf. *simplora* is most abundant at depths of 70-100 m on the Bulgarian shelf (Varna Bay). Pavel et al., (2021) provide the first account of soft-walled monothalamous foraminifera, in particular representatives of the families Saccamminidae and Allogromiidae, as well as gromiids on the Romanian continental shelf (depths 19.5 to 149 m). Based on our own data and data available for the coastal area of Bulgaria (Temelkov, Golemansky and Todorov 2006; Golemansky, 1974; Golemansky 1999a, b) and Romania (Pavel et al., 2021), we conclude that the Black Sea fauna of soft-walled foraminifers is much more diverse than presently appreciated and distributed across a wide range of depths in different regions. Moreover, some species are associated with specific areas, depths and biotopes, while others are eurybiontic forms. For example, representatives of the genus *Psammophaga* have a wide geographical distribution in the Black Sea. According to our data, they inhabit the shelves of Bulgaria, the Caucasus, Türkiye, western, southwestern and southern Crimea (Tarkhankut, Donuzlav and Laspi Bay, bays of Sevastopol) as well as the Sea of Azov and Sivash Gulf. They dominate the meiobenthos at a depth of 142-260 m in the south-western part of the Crimean Peninsula, reaching a density of 86-116 thousands ind./m². Soft-walled foraminifers, primarily *Psammophaga* cf. *simplora*, are included among meiobenthos subdominants in the area of methane gas seeps at a depth of 77-172 m in the south-western part of the Crimean Peninsula (Sergeeva, 2003; Revkov and Sergeeva, 2004).

The species *Vellaria pellucida* and *V. sacculus* are also widespread in coastal waters. We have found that these species are most frequent and occur in the highest abundances (up to 110 thousand individuals/m² and higher) in fine sand and silty sediments. *Goodayia rostellata* is another widespread species found both in shallow and deep waters in the Black Sea. However, most of the Black Sea soft-walled foraminiferal species that we investigate are still rare and inhabit water depths of 120 m and more. Four representatives of the peculiar soft-walled foraminiferal genus *Nemogullmia* were found for the first time in the Black Sea in different areas described as new species: *N. pontica*, *N. bosphorica*, *N. longissima* and *Nemogullmia* sp. These monothalamous foraminifera, which have a body length up to 3 mm, need to be included not only in meiobenthos but also in macrobenthos. The taxonomic study of soft-walled foraminifera is far from complete and new species are expected to be identified and described in the future.

Unfortunately, our knowledge of the taxonomic diversity of the gromiids in the Black Sea and the Sea of Azov is even more incomplete. This group has been largely neglected and there are no publications devoted to the study of systematics of this group in the Black Sea and the Sea of Azov. Information about species of *Gromia* in this region has so far been limited to a few works that consider their spatial and bathymetric distribution, with an estimation of their contribution to the total density of benthic protozoans taxocenoses and the meiobenthos in general (Sergeeva and

Anikeeva, 2006; Sergeeva and Mazlumyan, 2015, Sergeeva et al., 2012, 2017). Noteworthy is the fact that the most abundant species in the Black Sea, *Gromia* sp. A, which inhabits both mussel collectors and soft sediments in the Black Sea shallows (Sergeeva and Anikeeva, 2006: 'Allogromiidae gen. sp. A'), is morphologically similar to *Gromia pyriformis*, recorded in the deep Arabian Sea in the Oxygen Minimum Zone (OMZ) (Gooday and Bowser, 2005). However, genetic data are required in order to confirm its identity.

It should be noted that some Black Sea gromiids reach 3 – 4 mm in diameter, and should therefore be considered as an important component of the macrobenthos. In addition, their biomass, which we determined at some stations, was 1.5–2 times higher than the biomass of macrofauna. However, researchers have not considered them as protozoans and have not included them in macrobenthos communities. In our surveys in the Black Sea, gromiids are recorded not only in bottom sediments but also associated with some macroalgae.

CHAPTER 5
TAXONOMIC REVIEW OF THE SOFT-WALLED
MONOTHALAMOUS FORAMINIFERA IN THE BLACK SEA AND
THE SEA OF AZOV

5.1. General characteristics of morphology of soft-walled foraminifera

Representatives of soft-walled foraminifera encompass morphologically diverse forms ranging from rounded tests to those with filiform tests. Gooday, (2002) identified 10 major morphotypes of foraminifera with organic test (Fig. 5.1). One of the main differences that has taxonomic significance is the number of apertures. According to this feature, monothalamous soft-walled foraminifera can be divided into those that have a single terminal aperture and those that have two apertures at opposite ends of the test. Other distinguishing morphological features include the shape and size of the test, the presence or absence of agglutinating particles on its surface, as well as the characteristics of the cell body, notably its color, homogeneity, the presence (absence) of a nucleus, its size and location in the cell, and the presence of organic and mineral inclusions. However, genetic data show that most features of monothalamid test morphology have little phylogenetic significance.

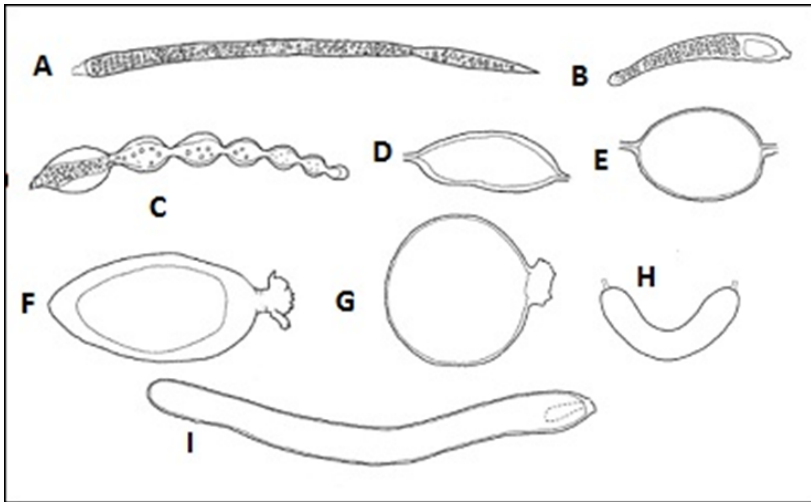


Figure 5.1. Organic-walled allogromiid morphotypes (after Gooday, 2002): A – elongate *Nodellum*-like form with pointed proloculus. B– *Nodellum*-like form. C – *Resigella moniliforme* Resig, 1982. D – *Tinogullmia riemanni* Gooday, 1990; E – species with two opposing apertures. F – *Vellaria pellucida* Gooday & Fernando, 1992. G – spherical species. H – *Tinogullmia*-like species. I – elongate species.

5.2. Taxonomic composition of soft-walled foraminifera in the Black Sea and the Sea of Azov

Based on literature sources and our own data, the fauna of this foraminiferal group in the Black Sea and the Sea of Azov is represented by 17 species (Table 5.1, Fig. 5.2), 27 morphospecies (described to genus, in total 23 genera), and 67 morphotypes (identified to the families Allogromiidae and Saccamminidae).

Table 5.1. List of soft-walled foraminifera species in the Black Sea and the Sea of Azov *

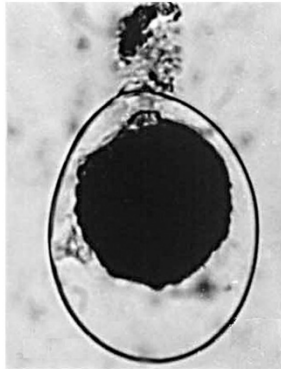
Species	Year of discovery	Source
<i>Hippocrepinella hirudinea</i> Heron-Allen et Erland, 1932	1968	Mikhalevich, 1968
<i>Lagynis pontica</i> Golemansky, 1999	1970	Golemansky, 1999
<i>Vellaria pellucida</i> Gooday & Fernando 1992*	1986	Sergeeva and Anikeeva, 2004
<i>Vellaria sacculus</i> Gooday & Fernando 1992	2004	Sergeeva and Anikeeva, 2006
<i>Tinogullmia lukyanovae</i> Gooday, Anikeeva et Sergeeva, 2006	1986	Gooday, Anikeeva and Sergeeva, 2006
<i>Tinogullmia</i> cf. <i>riemanni</i> Gooday, 1990	2007	Sergeeva, Anikeeva and Gooday, 2010
<i>Psammophaga</i> sp. (<i>P.</i> cf. <i>simplora</i>)	1994	Gooday, Anikeeva and Pawlowski 2011
<i>Goodayia rostellata</i> Sergeeva & Anikeeva, 2008	2006	Sergeeva and Anikeeva, 2008
<i>Nellya rugosa</i> Gooday, Anikeeva & Pawlowski, 2011	2008	Gooday, Anikeeva and Pawlowski, 2011
<i>Cedhagenia saltatus</i> Gooday, Anikeeva & Pawlowski, 2011	2008	Gooday, Anikeeva and Pawlowski, 2011
<i>Guanduella podensis</i> Temelkov, 2010	2009	Temelkov, 2010
<i>Bellarium rotundum</i> Anikeeva, Sergeeva & Gooday, 2013*	2010	Anikeeva, Sergeeva and Gooday, 2013
<i>Krymia fusiformis</i> Anikeeva, Sergeeva & Gooday, 2013	2010	Anikeeva, Sergeeva and Gooday, 2013
<i>Nemogullmia bosporica</i> Sergeeva & Anikeeva, 2020	2016	Sergeeva and Anikeeva, 2020

<i>Nemogullmia pontica</i> Sergeeva & Anikeeva, 2020	2016	Sergeeva and Anikeeva, 2020
<i>Nemogullmia longissima</i> Sergeeva & Anikeeva, 2020	2016	Sergeeva and Anikeeva, 2020
<i>Vellaria solenta</i> Sergeeva & Anikeeva, 2021	2020	Sergeeva and Anikeeva, 2021

Vellaria sacculus *Lagynis pontica* *Cedhagenia saltata* *V.pellucida*



Nemogullmia bosporica



Psammophaga cf. simplora



Bellarium rotundum



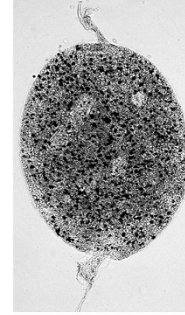
Tinogullmia lukyanovae



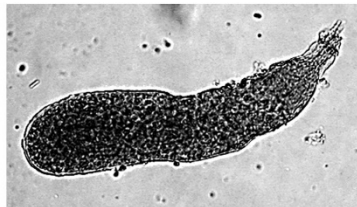
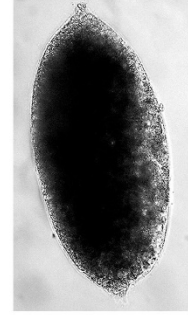
Vellaria solenta



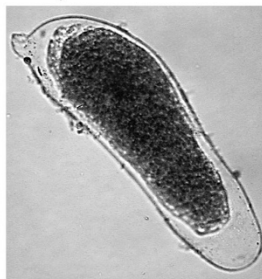
Goodayia rostellata



Guanduella podensis



Nemogullmia longissima



Nemogullmia pontica

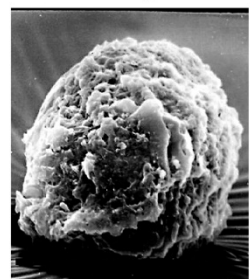


Figure 5.2. Organic-walled allogromiid morphotypes in the Black Sea

More than 60 representatives from various coastal and deep-water areas of the Black Sea are housed in the collection of the Institute of Biology of the Southern Seas of the Russian Academy of Sciences (Sevastopol) and require further detailed study (*incertae sedis*). It should also be noted that 3 of the 95 species found in the Black Sea were observed only in the mussel mariculture.

Soft-walled foraminifers, notably *Psammophaga* cf. *simplora*, were first recorded in the meiobenthos collections of the Sea of Azov in 2001 (Sergeeva N.G., unpublished data). This species was not abundant but was observed at 8 stations characterized by different salinity conditions. Off-season surveys of monothalamous foraminifers of the southwestern part of the Sea of Azov, adjacent to the northern coast of Crimea (2016-2018), showed that these protozoans are a constant component of the meiobenthos of this water-body.

The first data on soft-walled foraminifers of the Sivash Bay (the Sea of Azov) were obtained in 2013 and 2015. Due to the sharp salinization of the bay waters, a meiobenthos study was carried out at several coastal stations along the salinity gradient. This revealed that the Sea of Azov, including Sivash, hosts four monothalamid species - *Bellarium rotundum* Anikeeva, Sergeeva & Gooday, 2013, *Vellaria* cf. *pellucida* Gooday & Fernando, 1992, *V. solenta* Sergeeva & Anikeeva, 2021, *Psammophaga* cf. *simplora* Arnold, 1982 and at least 10 morphotypes. All of these species are common to the Sea of Azov and the Black Sea. The study of these benthic protozoans is far from being completed and new species are expected to be identified and described in the future. Undoubtedly, the species richness of the soft-walled foraminifera of the Black Sea and the Sea of Azov will be even more significant in future studies.

In the preparation of this book, our main goal was to provide benthic specialists with accessible and sufficiently complete information about a little-known group of benthic protozoans in the Black Sea and the Sea of Azov, which are presently unknown to many researchers of benthic communities. The information presented on the contribution of this group of protozoa to meiobenthic communities will allow a better understanding of their role in the functioning of bottom ecosystems and biogeochemical cycling of substances in these habitats.

We present below a brief morphological description of the SWF species and most of the morphotypes that we recorded, their ecological and biotopic preferences and, where possible, new data on the distribution of SWF in some areas with an estimation of their contribution to benthic communities. The diagnoses and illustrations of soft-walled foraminifera presented in the book give an understanding of them as part of the bottom communities of soft sediments and the meiobenthos of mussel mariculture. Since many soft-walled foraminifera could not be assigned to any known genus, we gave them provisional names identifying them as belonging to either the Saccamminidae or Allogromiidae, e.g., *Saccamminid* sp. 8, *Allogromiid* sp. 4, *Allogromiid* sp. D, *Saccamminid* sp. A. This kind of informal nomenclature has been used in many works, including the we have co-authored (Sergeeva and Anikeeva, 2006; Gooday et al., 2005; Radziejewska et al., 2006; Sergeeva, Anikeeva and Gooday, 2010).

5.3. Morphological review of the soft-walled foraminifera of the Black Sea and the Sea of Azov

Phylum Foraminifera d'Orbigny 1826.
Class of Monothalamea Haeckel, 1862.
Order Astrorhizida Brady, 1881.
Suborder Saccamminina Lankester, 1885.
Superfamily Saccamminoidea Brady, 1884.
Family Saccamminidae Brady, 1884.
Subfamily Saccammininae Brady, 1884.

Genus *Psammophaga* Arnold, 1982

Diagnosis of genus: A pear-shaped or egg-shaped monothalamid with an organic shell covered externally with agglutinating material. It has one simple aperture located at the narrowed end of the test. Cytoplasm contains mineral particles that are collected by the protozoan and remain within the cell body throughout life.

***Psammophaga* sp.** (Gooday, Anikeeva & Pawlowski 2011)

(Syn.: *Psammophaga simplora* [Anikeeva, 2005a; Sergeeva & Anikeeva 2006] (Fig. 5.3)

Description. The test is, more or less elongated and ranging from 250 to 430 μm long and 125 to 220 μm wide with a coefficient *C* of about 2 and resembles a grain of wheat. It has a more or less elongate shape, similar to that of a grain of wheat. The single aperture is located at the pointed end of the test and appears to be a simple round hole, sometimes on a short neck (Fig. 5.3. B). The diameter of the aperture varies from 14 to 28 μm . The wall is 3 – 6 μm thick, flexible, and translucent (Fig. 5.3. A). The cytoplasm contains large amounts of stercomata (waste material) and mineral particles, most of which are concentrated near the aperture. The diameter of the nucleus is 30-60 μm . Due to the large accumulations of various inclusions in the cell, the nucleus is not visible in all specimens. A characteristic feature of this species is the presence of diatom fragments inside the test.

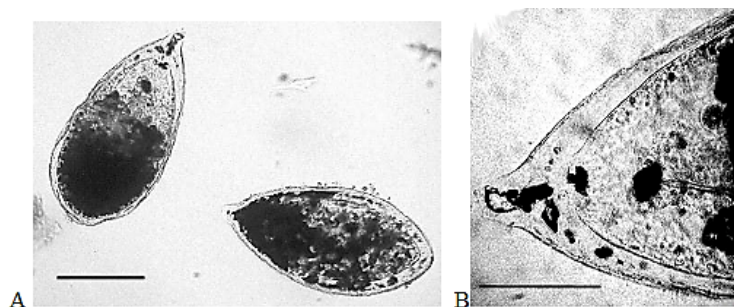


Figure 5.3. *Psammophaga* sp.: A—general view, B—aperture (Scale bars: A—100 μm , B—50 μm)

Differential diagnosis. The Black Sea *Psammophaga* sp. was initially identified as *P. simplora* (Anikeeva, 2005a) because there was no apparent difference from the type specimen. The length of the test of the type specimen described from the California coast is 250-350 μm , and the wall thickness of the test varies from 6 to 10 μm . We calculate that the coefficient *C* for the type specimen is about 1.5. Later, data on new representatives of the genus *Psammophaga* from different areas of the world ocean, including western Antarctica, Chile and the Adriatic Sea, have been published (Pawlowski and Majewski, 2011; Gschwend et al., 2016; Sabbatini et al., 2016). The new species share morphological features not only with the Black Sea *Psammophaga*, but also with each other. Since their identification as distinct species was confirmed by molecular analysis, the taxonomic status assigned to them is not in doubt. In view of this, at this stage it was decided to identify the Black Sea *Psammophaga* only to the genus level (Gooday, Anikeeva & Pawlowski, 2011).

Distribution. This species is more common in muddy sediment, sand. It is widely distributed in the Black Sea: it is common on the shelf of Bulgaria, the Caucasus, in the area of the Zernov's Phyllophora Field, Donuzlav Bay, bays of Sevastopol, the southern coast of Crimea and the Sea of Azov. It is found in significant densities across a wide range of depths (from 6 to 110 m and more).

***Psammophaga* sp. 1** (Sergeeva, Anikeeva & Gooday, 2010)
(Fig. 5.4).

Description. The test varies from 300 to 330 μm in length and 115-145 μm in width; coefficient *C* is 2.4 on average. The wall is rather thick and agglutinated with fine sandy material mixed with detritus. The aperture is located at the narrower end of the test and is a simple hole associated with a projecting capsule-like structure, measuring 18 μm long and 25 μm wide. The cytoplasm contains mineral particles, as in all *Psammophaga* species (Fig. 5.4).

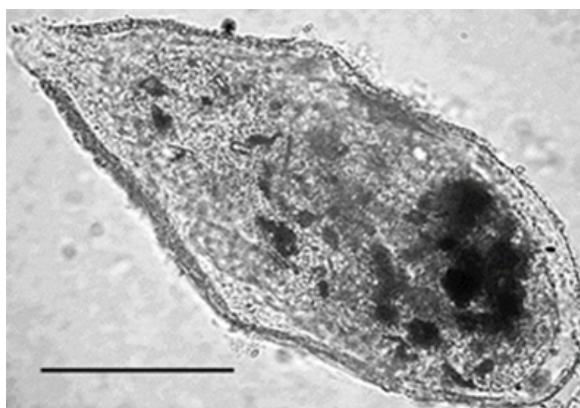


Figure 5.4. *Psammophaga* sp. 1 (Scale bar: 100 μm)

Differential diagnosis. Unlike *Psammophaga* sp., this species has a thicker agglutinated test and a capsule-shaped formation with an aperture at the end.

Distribution. Representatives of *Psammophaga* sp. 1 are found on the open coast of the Black near Sevastopol at a depth of 13 m, and in the Dnieper Canyon area at 150-160 m. The species is confined to sandy silt with an admixture of broken mollusc shells and to coarse quartz sand.

***Psammophaga* sp. 2** (Anikeeva et al., 2019)

(Fig. 5.5)

Description. This form is referred to *Psammophaga* based on its main features: the shape of the test, which measures 220 x 95 μm with a coefficient *C* of 2.3 (Fig. 5.5 A), the finely agglutinated test wall, the single aperture and associated apertural structure measuring 15x30 μm (Fig. 5.5 B), and the presence of mineral particles in the cytoplasm. The nucleus, diameter 18 μm , is clearly visible close to the centre of the cell body.

Differential diagnosis. The main feature that distinguishes *Psammophaga* sp. 2 from *Psammophaga* sp. and other Black Sea psammophagids is funnel-like apertural structure.

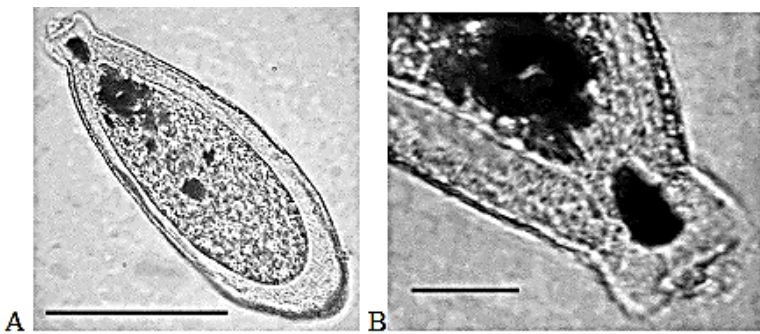


Figure 5.5. *Psammophaga* sp. 2: A - general view, B - aperture
(Scale bars: A – 100 μm , B – 20 μm)

Distribution. The species is found in the Dnieper Canyon in the area of the northwestern Black Sea (in the zone with low level of O_2) at a depth of 120 m on thin phaseoline silt, and in the Karkinitzky Gulf at a depth of 34 m on silt with mollusc shell debris.

***Psammophaga* sp. 3**

(Fig. 5.6)

Description. The test is oval, measuring 350 x 224 μm with a coefficient *C* about 1.5. It is slightly pointed at the apertural end, while the opposite end is rounded and slightly narrower (Fig. 5.6A). The aperture is simple and the associated structure, diameter is 20 μm , is typical of the genus (Fig. 5.6B). The wall is thin, transparent, with finely dispersed agglutination. The cytoplasm is evenly distributed throughout the test cavity and contains a large accumulation of rounded transparent inclusions

with a diameter of about 20 μm . Characteristic mineral inclusions are visible in the anterior half of the test.

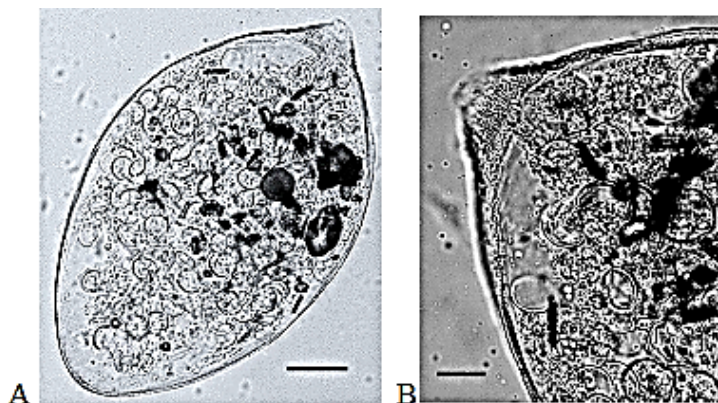


Figure 5.6. *Psammophaga* sp. 3: A – general view, B – aperture (Scale bars: A – 50 μm , B – 20 μm).

Differential diagnosis. Features that distinguish *Psammophaga* sp. 3 from *Psammophaga* sp. and other species of this genus are the unusual content of protoplasm and the very thin test wall, which is not typical for *Psammophaga* or for other members of the Saccamminidae.

Distribution. The species is found in the Bosphorus region of the Black Sea at a depth of 296 m in black fluid silt with a strong smell of hydrogen sulfide at a depth of 2 cm.

***Psammophaga* sp. 4**

(Fig. 5.7)

Description. The test is oval, average size 293 x 147 μm and coefficient *C* about 2.0. The apertural structure resembles a capsule, 30 x 15 μm in size. The test wall is dense and agglutinated. The protoplasm is separated from the wall by a small space (about 12 μm) and filled with mineral inclusions, most of which are concentrated at the posterior end of the cell (Fig. 5.7).

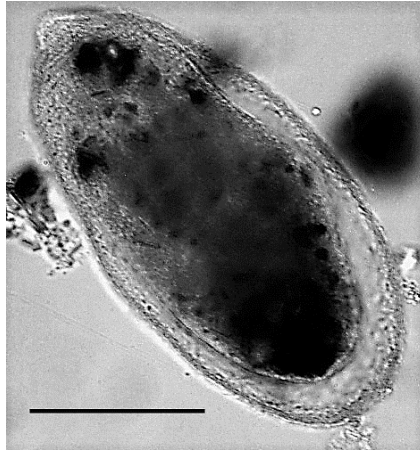


Figure 5.7. *Psammophaga* sp. 4 (Scale bar: 100 μm)

Differential diagnosis. In terms of its aperture structure, this species somewhat resembles *Psammophaga* sp. 1, but the difference in the shape of the test and the structure of the wall distinguishes the two species.

Distribution. The species is found in the Black Sea near the Istanbul Strait (Bosporus) at a depth of 150 m in red oxidized silt. It is confined to the surface 1 cm layer.

***Psammophaga* sp. 5**

(Fig. 5.8)

Description. The test is oval, slightly elongated along the longitudinal axis, and measures 410 x 200 μm with a coefficient C of about 2. The aperture is located at the end of a small neck, size 25 x 35 μm . The test wall is thin, proteinaceous, transparent, and double-layered. The cytoplasm tightly adjoins the test wall, filling the entire test space. It is filled with stercomats and mineral particles, most of which are located closer to the aperture (Fig. 5.8).

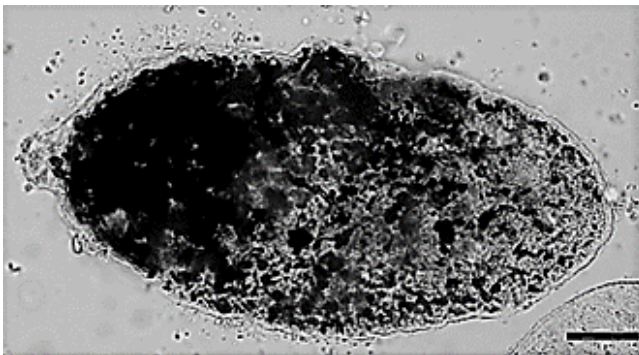


Figure 5.8. *Psammophaga* sp. 5 (Scale bar 50 μm)

Differential diagnosis. *Psammophaga* sp. 5, as well as *Psammophaga* sp. 3, are distinguished from other Black Sea psammophagids by their thin-walled test. However, the presence of mineral particles in the cell, as well as the test shape and the nature and location of the aperture, make it possible to identify it as a representative of this genus. This species differs from *Psammophaga* sp. 3 in shape of the test and absence of round transparent inclusions in the cytoplasm.

Distribution. The species is found in the Sea of Azov at a depth of 8-11 m under hypoxia conditions.

Genus *Cedhagenia* Gooday, Anikeeva & Pawlowski, 2011

Diagnosis of genus: Test free, monothalamous, approximately lenticular in shape with curved sides and more or less pointed ends; length 150-300 μm . Single aperture sometimes associated with short, delicate, transparent, slightly flared test extension. Test collapses when dried. Wall flexible, whitish, translucent with shiny highlights; composed of inner organic layer overlain by small (usually $<5 \mu\text{m}$ in size) plate-like mineral grains. Cytoplasm finely granular, without stercomata.

Cedhagenia saltatus Gooday, Anikeeva & Pawlowski, 2011

(Fig. 5.9)

Description. The test is more or less lenticular in shape, expanding in the middle, and ranging from 147 to 294 μm in length, 65 to 153 μm in width, coefficient *C* 1.6 to 2.9 (Fig. 5.9). The apertural structure is wide and usually slightly fringed at the end. The test wall is dense, semi-transparent, about 15 μm thick, and comprises an inner organic layer covered with agglutinated particles. The cytoplasm fills most of the test space and contains vacuole-like inclusions.

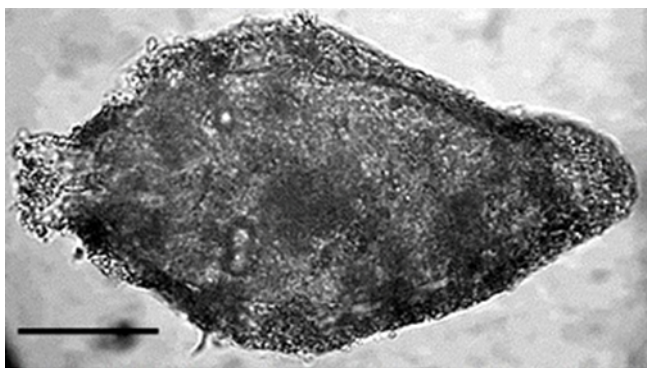


Figure 5.9. *Cedhagenia saltatus* (Scale bar 50 μm)

Differential diagnosis. Morphologically, the new genus is most similar to *Vellaria*, notably in the presence in some specimens with a delicate, flared apertural extension. However, this structure is not as well developed as in *Vellaria* and the overall test shape is also more lenticular. Molecular analyses indicate that *Cedhagenia* is not related to *Vellaria pellucida*, a typical representative of the genus. Instead, they suggest that the new genus is most closely related to *Ovammina*. Morphologically, it

differs from the type species, *Ovammina opaca*, in having a much thinner wall and a generally distinct apertural structure.

Distribution. The species is found in the Black Sea near Sevastopol (Balaclava Bay) in dark sandy silt at a depth of 3 - 5 m.

Subfamily Colonammininae Rauzer-Chernousova & Reitlinger, 1993

Genus *Conqueria* Gooday & Pawlowski, 2004

Diagnosis of genus: The test is monothalamous, elongated, tubular in shape, 300-1000 μm and more in length and 50-100 μm in width. The aperture is simple, located at the end of the short terminal neck. The outer surface of the test wall is very finely and homogeneously agglutinated.

***Conqueria* sp. 1** (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.10).

Description. The test is long and slightly curved (Fig. 5.10 A), measuring 310 x 50 μm with a coefficient *C* of 6.2. The aperture is located on the end of the short neck (Fig. 5.10 B) that is 12 μm long and 22 μm wide. The wall is finely and uniformly agglutinated. The cytoplasm is homogeneous and fills the entire test space except at the apertural end.



Figure 5.10. *Conqueria* sp. 1: A – general view, B – aperture; (Scale bars: A – 50 μm , B – 20 μm)

Differential diagnosis. This specimen is morphologically similar to *Conqueria laevis*, described from the abyssal zone of Weddell Sea (Gooday and Pawlowski, 2004a).

Distribution. It is found in the northwestern part of the Black Sea at a depth of 150 m in sandy silt with an admixture of bivalve shells and at a depth of 56 m in silted fine sand with detritus.

Class Monothalamea Haeckel, 1862

Genus *Nellya* Gooday, Anikeeva & Pawlowski, 2011

Diagnosis of genus: Test free, monothalamous, elongate, more or less oval in shape; proximal end rounded to bluntly pointed, distal end often rather truncated; length <400 μm . Single aperture associated with transparent, roughly rectangular, nipple-like projection located at distal end. Test wall almost opaque, whitish and flecked with darker grains, somewhat flexible and rough on a scale of tens of microns;

wall is comprised of inner organic layer overlain by jumble of mineral grains, most of them ~10 µm in size or smaller. Cytoplasm without stercomata.

Nellya rugosa Gooday, Anikeeva & Pawlowski, 2011
(Fig. 5.11)

Description. The test is approximately oval, somewhat reminiscent of a short cigar or a rice grain, and usually slightly flattened (Fig. 5.11A). It ranges from 118 to 365 µm in length, 59–212 µm in width, with a coefficient *C* of 1.22 to 2.71. The sides are gently curved and taper towards the narrowly rounded or bluntly pointed proximal end (Fig. 5.11C). The apertural end (Fig. 5.11B) is broadly rounded and often more or less truncated. A transparent, nipple-like apertural structure, approximately rectangular in shape and varying in its degree of prominence, protrudes from this end. The actual aperture is not obvious but is presumably located in the centre of this structure. The test wall is ~20 µm thick, fairly flexible and comprises an inner organic layer overlain by agglutinated particles. It is fairly opaque, whitish, and flecked with scattered darker (black and greenish) grains. When dried on an SEM stub, the test flattens so that the shape appears broader. However, it does not collapse completely, except for the apertural structure, which is entirely organic in composition and disappears when dried. Most of the agglutinated particles are transparent but there are also some scattered black grains. Viewed in the SEM, the test surface is uneven on a scale of tens of microns, and comprises a loose jumble of particles arranged with no apparent order. Most of the larger particles are <10 µm in size, angular/subangular in shape and presumably quartz, but some plate-like grains, possibly mica, are also present. One or two larger grains, several tens of microns in size and sometimes plate-like, may also be present. Smaller grains, which again include some platelike particles (probably clay minerals), fill in the spaces between the larger grains. The interior of the test is not clearly visible through the wall, which is more or less opaque, even when immersed in glycerol. However, large inclusions, such as mineral grain or stercomata, do not appear to be present.

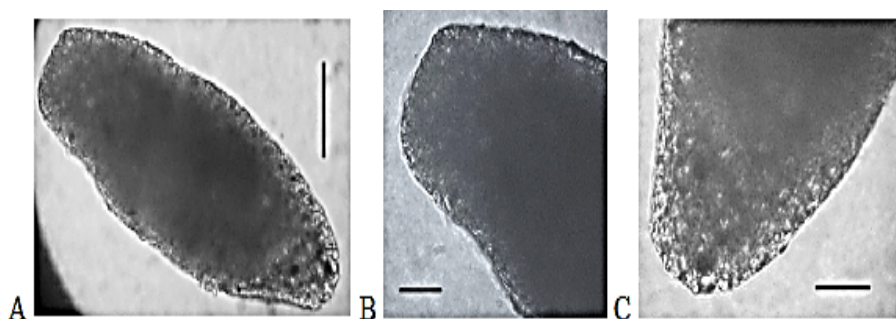


Figure 5.11. *Nellya rugosa*. A-general view, B - apertural part, C - opposite part (Scale bars: A – 50 µm, B, C – 20 µm)

Differential diagnosis. The new genus differs from *Saccamina* and *Leptamina* in the shape of the test (elongate rather than approximately spherical) and the presence of a nipple-like apertural structure, which is quite unlike the simple

round opening that characterises these two genera. Compared with the new genus, *Conqueria* has a more elongate test, a finely agglutinated wall and an aperture located at the end of a short tube. The test shape, apertural structure and the absence of intracellular mineral grains distinguishes *Nellya* from *Psammophaga*. The general shape of the test is similar to that of *Vellaria*, but the apertural structure is completely different. Molecular analyses confirm that it is a distinct genus (Gooday et al., 2011).

Distribution. The species is found in the Black Sea near Sevastopol (Balaklava Bay) in dark sandy silt at a depth of 3 - 5 m.

***Nellya* sp.** (Anikeeva et al., 2019)
(Fig. 5.12).

Description. The test is elongate, approximately oval (Fig. 5.12), 220 μm long, 79 μm wide with the coefficient *C* of 2.8 in the figured specimen. The single rounded aperture (~15 μm diameter) is located at the narrower end of the test. The wall is rather thick and agglutinated, becoming thinner at the apertural end.

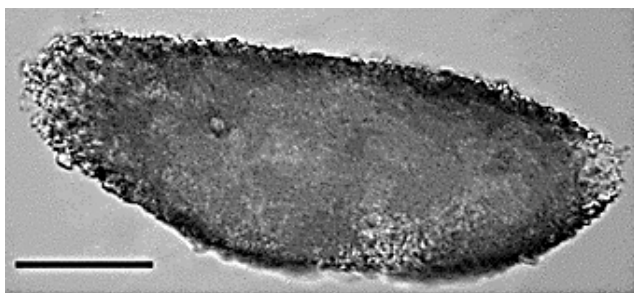


Figure 5.12. *Nellya* sp. (Scale bar: 50 μm)

Differential diagnosis. The genus *Nellya* was described from 5-10 m in Balaklava Bay (Gooday et al., 2011). The present specimens closely resemble the type species, *N. rugosa* Gooday, Anikeeva & Pawlowski 2011, and may be conspecific with it. However, its occurrence in deeper water, the different form of the apertural end (broadly rounded and often more or less truncated in *N. rugosa*), and the absence of an obvious nipple-like apertural projection, lead us to separate this form under open nomenclature for the present.

Distribution. This species is found in Feodosiya Gulf at 22 m depth. It inhabits silt mixed with sand and seashells.

Saccamminid sp. 1 (Sergeeva, Anikeeva & Gooday, 2010)
(Fig. 5.13).

Description. The test is elongated and more or less cylindrical, 470 μm long and 130 μm wide with a coefficient *C* of 3.6. (Fig. 5.13A). A single prominent apertural structure (Fig. 5.13B) measures 40 μm long and 40 μm wide. The wall is finely agglutinated. The cytoplasm is finely granular, homogeneous and does not fill the entire space of the test.

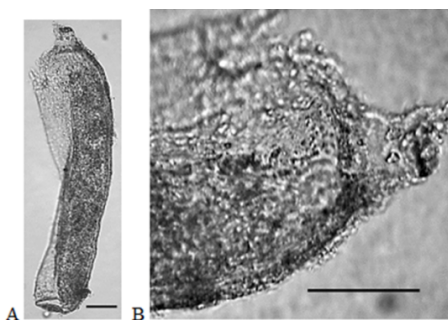


Figure 5.13. Saccamminid sp. 1: A – general view, B-apertural part; (Scale bars: 50 µm)

Differential diagnosis. Morphologically, this representative cannot be assigned to any known genus within the family Saccamminidae.

Distribution. It is found in the northwestern part of the Black Sea at a depth of 160 m in quartz sand with an admixture of silt and mollusc shells.

Saccamminid sp. 2 (Sergeeva, Anikeeva & Gooday, 2010)
(Fig. 5.14).

Description. The single specimen is 175 µm long and 80 µm wide with a coefficient C of 2.2. The test is rather elongate and resembles a prolate spheroid. It is widest in the middle and tapers towards the two bluntly pointed ends (Fig. 5.14). Two bulbous apertural structures, 11 µm long and 20 µm wide, are situated symmetrically at opposite ends of the test. The agglutinated wall is fairly thick but becomes thinner on the apertural structures. The cytoplasm contains some dark inclusions as well as transparent particles, most likely quartz.

Differential diagnosis. Saccamminid sp. 2 has some similarities with the genus *Amphitremoida*, notably the presence of two apertures and the thick agglutinated test wall. However, significant differences, for example, the different body shape and the aperture structures, distinguish it from this genus. The Black Sea specimen also has common features with Saccamminid sp. 29 (Gooday et al., 2005), but the species we describe has a thicker wall, apertures in the form of capsules and irregularly oval test shape.



Figure 5.14. Saccamminid sp. 2 (Scale bar: 50 µm)

Distribution. The species is found within the hypoxic zone of the north-western Black Sea at a depth of 150 m in silty sand with an admixture of bivalve shells. Similar organisms are often found in deep water samples from other seas (Gooday et al., 2004b).

Saccamminid sp. 3 (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.15).

Description. The test is large, broadly oval in shape (Fig. 5.15A), 460 μm long and 270 μm wide with a coefficient C of 1.7. The aperture is wide and located at the end of a short neck (Fig. 5.15B), measuring 57 μm long and 57 μm wide. The test wall is thick, agglutinated with fluffy detritus. The cytoplasm is dense and homogeneous. There is a barely discernible canal (Fig. 6.15C) on the opposite end of the test.

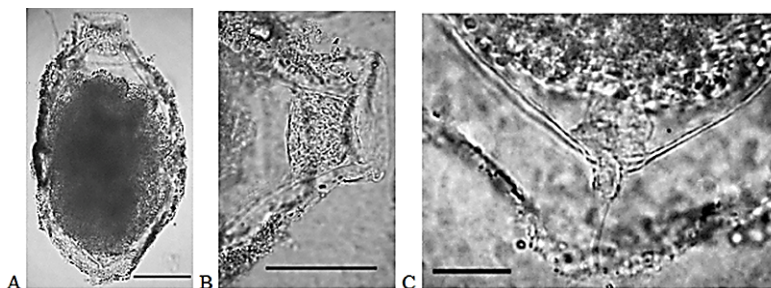


Figure 5.15. Saccamminid sp. 3: A – general view, B – aperture, C – opposite part of the test (Scale bars: A, B – 50 μm , C – 20 μm).

Differential diagnosis. The morphological features of Saccamminid sp. 3 are not consistent with any of the known saccamminid genera.

Distribution. This species is found in the hypoxic zone of the northwestern part of the Black Sea at a depth of 150 m in silty sand with admixture of broken bivalve shells.

Saccamminid sp. 4 (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.16).

Description. This species has an elongate oval test (Fig. 5.16A), 330 μm long and 120 μm wide, with a coefficient C of 2.7. The simple aperture (Fig. 5.16B) is 15 μm wide and located at the bluntly pointed end. The test wall is relatively thick and finely agglutinated. There is a single nucleus, 28 μm diameter.



Figure 5.16. Saccamminid sp. 4: A – general view, B – aperture; (Scale bars: A – 50 μm , B – 20 μm)

Differential diagnosis. Saccamminid sp. 4 is similar to the genus *Psammophaga* in the shape of the test and the presence of a single aperture. However, the absence of mineral inclusions in the cytoplasm, the thickness of the test wall and the homogeneous structure of the granular cytoplasm are features that distinguish it from *Psammophaga*.

Distribution. This species is found in the NW Black Sea at a depth of 120 m in fine silt with an admixture of the broken *Phaseolina* shells.

Saccamminid sp. 5 (Anikeeva & Gooday, 2016)

(Fig. 5.17)

Description. The test is elongate, measuring 443 x 156 μm with a coefficient *C* of 2.8. The single aperture is located at the wider end of the test; it has diameter of about 32 μm and a slightly ragged edge. The wall is densely agglutinated (Fig. 5.17). The cytoplasm is granular, homogeneous and does not fill all the space within the test.

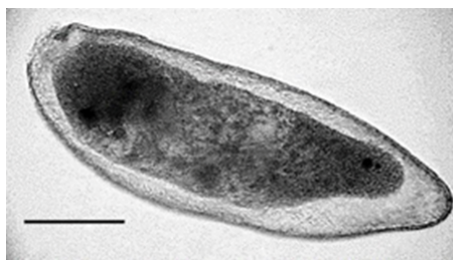


Figure 5.17. Saccamminid sp. 5 (Scale bar: 100 μm)

Differential diagnosis. This species resembles Saccamminid sp. 28 in the shape of the test and wall thickness. However, the two species can be distinguished by substantial differences in the structure of the aperture.

Distribution. Saccamminid sp. 5 was found in the Black Sea in the area of the Zernov's *Phyllophora* field at a depth of 24 m on silty sand with mollusc shell fragments, and in the area of Cape Opuk at a depth of 95 m in the silt with dead shells of the *Phaseolina*.

Saccamminid sp. 7 (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.18).

Description. The test 250 μm long and 150 μm wide, and coefficient *C* of 1.6. It is very delicate, broadly oval, with a rather truncated distal end (Fig. 5.18 A). One large aperture is located at the end of a short, broad structure, 60 μm wide (Fig. 5.18 B).

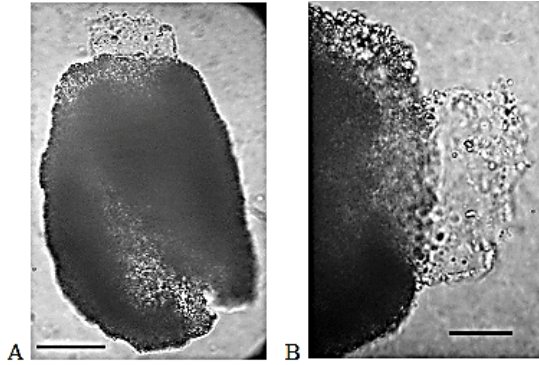


Figure 5.18. Saccamminid sp. 7: A – general view, B – aperture (Scale bars: A – 50 μm , B – 20 μm)

Differential diagnosis. Morphologically, this species cannot be assigned to any known saccamminid genus.

Distribution. It is found in the NW Black Sea at a depth of 120 m in fine *Phaseolina* silt.

Saccamminid sp. 8 (Sergeeva, Anikeeva & Gooday 2010)

(Fig. 5.19).

Description. The test is rather irregularly oval, 240 μm long and 90 μm wide with a coefficient C of 2.6 (Fig. 5.19 A). There is a single aperture, ~ 10 μm diameter, located at the slightly produced distal end (Fig. 5.19 B). The test wall is relatively thick and finely agglutinated. A single large nucleus, ~ 60 μm diameter, is located near the centre of the test. The cytoplasm is homogeneous, except for vacuole-like inclusions.

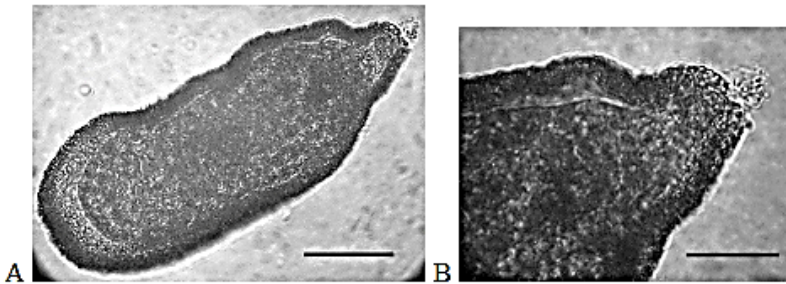


Figure 5.19. Saccamminid sp. 8: A – general view, B – aperture (Scale bars: A – 50 μm , B – 20 μm)

Differential diagnosis. This species differs from the genus *Psammophaga* in the absence of mineral particles in cytoplasm, as well as the shape of the test and the generally thicker wall. It cannot be assigned to any known saccamminid genus.

Distribution. The species is found in the NW Black Sea at a depth of 120 m in fine *Phaseolina* silt.

Saccamminid sp. 9 (Sergeeva, Anikeeva & Gooday, 2010)
(Fig. 5.20).

Description. The test is small, droplet shaped (Fig. 5.20A) with a broadly rounded proximal end and a narrowly rounded distal end. It varies from 190 to 260 μm long and 120 to 142 μm wide with a coefficient *C* of 1.7. The test wall is thick, finely agglutinated. The single aperture, located at the distal end, is 15-20 μm diameter (Fig. 5.20B). Cytoplasm contains many vacuoles.

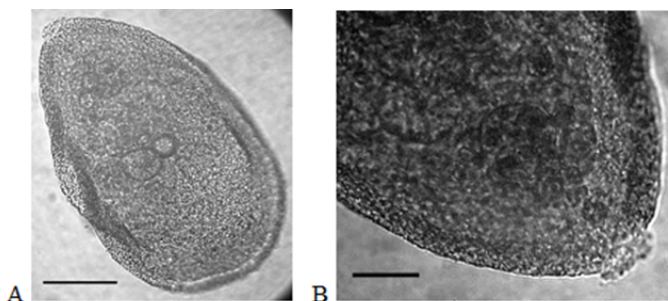


Figure 5.20. Saccamminid sp. 9: A – general view, B – aperture; (Scale bars: A – 50 μm , B – 20 μm)

Differential diagnosis. Saccamminid sp. 9 resembles the genus *Ovammina* in the shape of test, but differs from it in the structure of the test wall and aperture.

Distribution. This species is found in the northwestern part of the Black Sea at a depth of 120 m in fine silt with an admixture of the broken *Phaseolina* shells.

Saccamminid sp. 10 (Sergeeva, Anikeeva & Gooday, 2010)
(Fig. 5.21).

Description. The test is broadly and asymmetrically oval 350 μm long and 150 μm wide with a coefficient *C* of 2.3 (Fig. 5.21A). At either end, it is drawn out into two long and very delicate tubular extensions (45 μm long and 25 μm wide) with terminal apertures (Fig. 5.21B, C). The test wall is finely agglutinated. The cytoplasm content is not fully visible, but vacuole-like inclusions can be seen in some places.

Differential diagnosis. Morphologically, this species cannot be assigned to any known saccamminid genus.

Distribution. This species is found in the NW Black Sea at a depth of 120 m in fine *Phaseolina* silt.

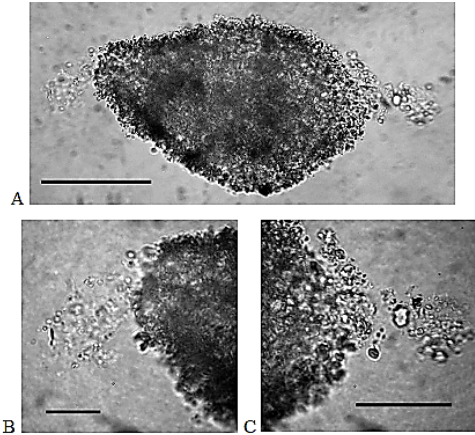


Figure 5.21. Saccamminid sp. 10: A – general view, B, C – apertures; (Scale bars: A – 100 μm , B – 20 μm , C – 50 μm)

Saccamminid sp. 11 (Sergeeva, Anikeeva & Gooday, 2010)
(Fig. 5.22).

Description. The test is relatively elongate and somewhat bottle-shaped (Fig. 5.22), with a bulbous proximal part tapering into a narrower distal part that ends in a simple aperture, diameter 16 μm . The length is 225 μm and the width 80 μm , with a coefficient C of 2.8. The test wall is thick, agglutinated. Finely granulated cytoplasm contains vacuole-like inclusions. There is a single nucleus, diameter 17 μm .

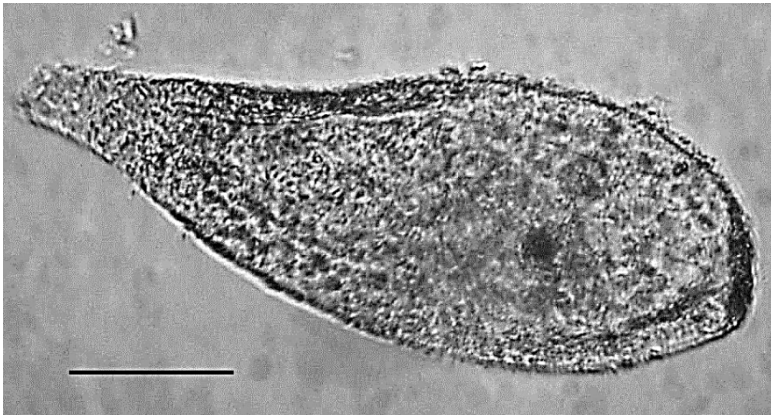


Figure 5.22. Saccamminid sp. 11 (Scale bar: 50 μm)

Differential diagnosis. Morphologically, this species is closest to the genus *Psammophaga*, but the test is more elongated and the cytoplasm is free of mineral particles.

Distribution. The species is found in the NW Black Sea at a depth of 160 m in silt with broken molluscs shells and quartz sand.

Saccamminid sp. 14 (Sergeeva, Anikeeva & Gooday, 2010)
(Fig. 5.23).

Description. The test is almost spherical, 200-210 μm diameter, with a wide, low apertural structure 20 μm long and 67 μm wide. The wall is thick but very fragile and composed of fine mineral particles (Fig. 5.23). There is a single nucleus, diameter 32 μm .

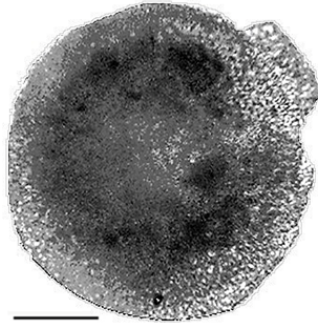


Figure 5.23. Saccamminid sp. 14 (Scale bar: 50 μm)

Differential diagnosis. Morphologically, this species cannot be assigned to any saccamminid genus.

Distribution. This species is found in the NW Black Sea at a depth of 130 m in fine phaseoline silt.

Saccamminid sp. C. [Syn. Saccamminidae gen. sp. C (Anikeeva et al., 2019)]
(Fig. 5.24)

Description. The test is symmetrical and broadly spindle-shaped (Fig. 5.24A); length 480 μm , width 234 μm with a coefficient C of ~ 2 . Two simple rounded apertures (diameter $\sim 28 \mu\text{m}$) are located at the bluntly pointed ends of the test. The test wall is finely agglutinated. The cytoplasm is relatively featureless except for a nucleus, diameter $\sim 50 \mu\text{m}$ (Fig. 5.24B). The cytoplasm is separated from the test wall by an empty space.

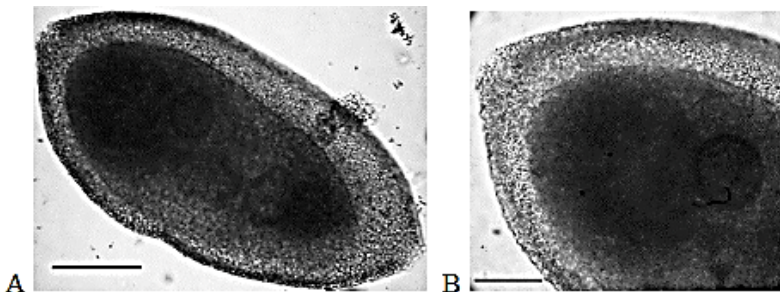


Figure 5.24. Saccamminid sp. C: A – general view, B – nucleus and one of the apertures
(Scale bars: A – 100 μm , B – 50 μm)

Differential diagnosis. Some deep-sea saccamminids with two terminal apertures have a similar shape to Saccamminidae sp. C (e.g., Gooday et al., 2004b, Figs 2A-D), but can be differentiated from this species by the nature of the cell body, which is characterized by the presence of numerous stercomata, as well as more complex apertural structures. There are interesting similarities between these kinds of broadly spindle-shaped saccamminids and the Palaeozoic monothalamid genus *Amphitremoida* (e.g. Nestell & Tolmacheva, 2004).

Distribution. This species was found for the first time at a depth of 14 m in Kazach'ya Bay (Sevastopol region) in sandy sediment with shell debris (unpublished data). Later we discovered this species in Kalamitskiy Gulf on 36 m in black silt with an admixture of broken mollusc shells.

Saccamminid sp. X [Syn. Saccamminidae gen. sp. X (Syrtlanova & Anikeeva 2007)]

(Fig. 5.25)

Description. The shape of the test varies from oval to rounded, measuring 230 x 130 μm with a coefficient *C* of 1.7. (Fig. 5.25). The single aperture, about 30-35 μm in diameter, is sometimes surrounded by a small fringe. The nucleus is not clearly visible due to the dense agglutination of the test wall. Its diameter is about 25 μm .

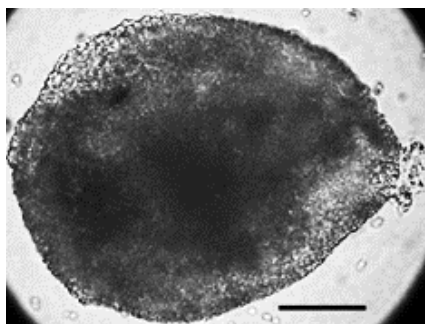


Figure 5.25. Saccamminid sp. X. (Scale bar: 50 μm)

Differential diagnosis. Morphologically, this representative cannot be assigned to any known saccamminid genus.

Distribution. The species is found on mussel collectors in Karantinnaya Bay (Sevastopol area, Black Sea).

Saccamminid sp. X₁ [Syn. Saccamminidae gen. sp. X₁ (Syrtlanova & Anikeeva 2007)]

(Fig. 5.26)

Description. The test is ellipsoidal, measuring 200 x 125 μm with a coefficient *C* of 1.6. The apertures are associated with two capsule-like structures, 23 μm in diameter, symmetrically located at the slightly narrowed ends of the test (Fig. 6.26). The wall is agglutinated. The cytoplasm is homogeneous, containing small vacuole-like inclusions.

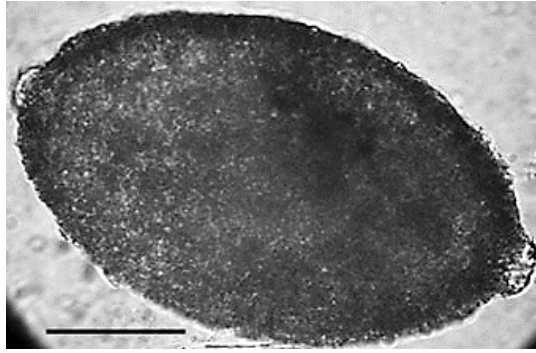


Figure 5.26. Saccamminid sp. X₁. (Scale bar: 50 μm)

Differential diagnosis. In terms of number and position of the apertures Saccamminid sp. X₁ is similar to the genus *Amphitremoida*, but differences in the shape of the test and the structure of the apertures distinguish the two taxa. This species is also similar to Saccamminid sp. C in terms of the test shape and the number of apertures. However, the nature of agglutination of the test wall, the content of cytoplasm and the structure of aperture distinguish them.

Distribution. The species is found on mussel collectors in Karantinnaya Bay (Sevastopol area, Black Sea).

Saccamminid sp. X₂ [Syn. Saccamminidae gen. sp. X₂ (Syrtlanova & Anikeeva 2007)]

(Fig. 5.27)

Description. The test is somewhat oval in shape, 270 x 170 μm in size with a coefficient *C* of 1.6. At one end it narrows, forming a kind of second chamber. The aperture is associated with an internal channel 14 μm in diameter, which is located at the wider end of the test. The wall is thick and agglutinated. A nucleus, 38 μm in diameter, is clearly visible in the center of the cell body (Fig. 5.27).



Figure 5.27. Saccamminid sp. X₂. (Scale bar: 50 μm)

Differential diagnosis. Morphologically, this species cannot be assigned to any known saccamminid genus.

Distribution. The species is found on mussel collectors in Karantinnaya Bay (Sevastopol area, Black Sea).

Saccamminid sp. Y (Sergeeva & Anikeeva, 2014; Anikeeva et al., 2019)
(Fig. 5.28)

Description. These species have a rather large test ranging from elongate to flask-like in shape, and from 300 to 700 μm long and from 140 to 300 μm wide with a coefficient C of 1.9-4. The dense wall is 2-5 μm thick and has a granular structure. The aperture is a wide opening, between 60 and 130 μm width depending on the test size, and is bounded by walls that are more finely agglutinated than the rest of the test. The nucleus diameter is 30-40 μm .

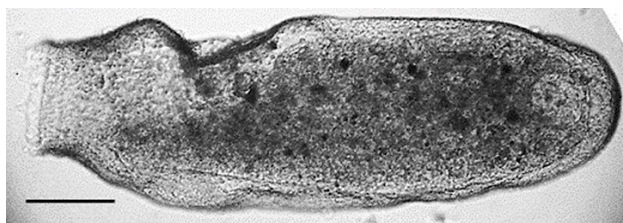


Figure 5.28. Saccamminid sp. Y (scalebar: 100 μm)

Differential diagnosis. Morphologically, this species cannot be assigned to any known saccamminid genus.

Distribution. The species is found in hypoxic sediments in Sevastopol Bay at a depth of 11-16 m. It is found also near Yalta, Feodosia, Cape Opuk, in the Karkinitzky Gulf in silty sediments with a broken phaseoline shells in the depth range of 22-95 m.

Saccamminid sp. 20 (Anikeeva & Gooday, 2016)
(Fig. 5.29)

Description. The test is elongated, oval in shape, and 432 x 186 μm in size with a coefficient C of 2.3. There is a single aperture, about 17 μm in diameter, located on a small projection at one of the ends of the test. The agglutinated wall is thick. The cytoplasm is granular, with vacuole-like inclusions and undefined dark-colored particles, and completely occupies the space within the test (Fig. 5.29).

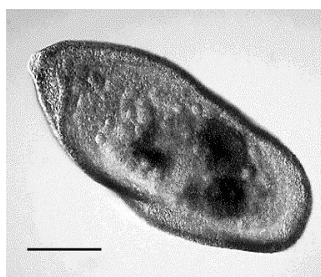


Figure 5.29. Saccamminid sp. 20 (Scale bar: 100 μm)

Differential diagnosis. Saccamminid sp. 20 has similarities with Saccamminid sp. 28 in terms of the shape and structure of the test, but there are differences in the structure of the apertures, the placement of the cytoplasm within the test and the cytoplasmic contents. Given these differences, we refer the two forms to different morphospecies.

Distribution. This species is found in the Black Sea in the area of the Zernov's *Phyllophora* Field (NW) at a depth of 24 m in silty sand with broken mollusc shells.

Saccamminid sp. 21 (Anikeeva & Gooday, 2016)

(Fig. 5.30)

Description. The test is large, 800 x 345 μm on average with a coefficient *C* of approximately 2.3. It ranges from elongate to oval, and narrows towards the apertural end (Fig. 5.30). The aperture, about 35 μm in diameter, is located on a long transparent neck (~80 μm long), located at the narrow end of the test. The agglutinated wall is thick, dark and composed of large quartz particles. The cytoplasm is not clearly visible.

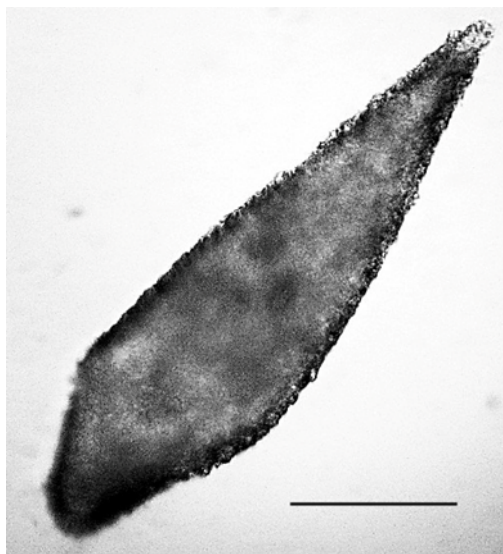


Figure 5.30. Saccamminid sp. 21 (Scale bar: 200 μm)

Differential diagnosis. Saccamminid sp. 21 cannot be referred to any known saccamminid genus.

Distribution. This species is found in the Black Sea in the area of the Zernov's *Phyllophora* field (NW) at a depth of 24 m in silty sand with a broken mollusc shells.

Saccamminid sp. 24 (Anikeeva et al., 2019)

(Fig. 5.31)

Description. The test is elongate, parallel-sided for most of its length with a rounded proximal end (Fig. 5.31); length 450 μm , width 100 μm , coefficient *C* is 4.5. The aperture forms a simple wide opening (diameter 65 μm) surrounded by a distinct

collar-like feature. The finely-agglutinated wall is 2-5 μm thick. The cytoplasm completely fills the test interior; it is relatively homogeneous except for the presence of a nucleus ($\sim 30 \mu\text{m}$ diameter), one obvious vacuole and several mineral grains.

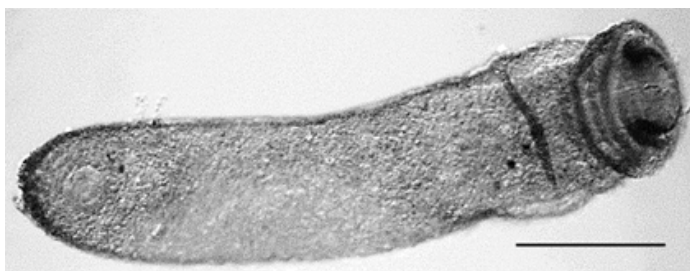


Figure 5.31. Saccamminid sp. 24 (Scale bar: 100 μm)

Differential diagnosis. Saccamminid sp. 24 is rather similar to Saccamminidae sp. Y of Sergeeva and Anikeeva (2014, Pl.3, Figs Q5, Q6) from Sevastopol Bay. The two forms are comparable in size, and both have a finely-agglutinated wall and a rather similar wide aperture associated with a collar-like feature. For the present, we distinguish them based on the much more elongate and cylindrical test shape in Saccamminid sp. 24, compared to the more rounded test of Saccamminidae sp. Y. However, it is possible that they represent variants of the same species. The elongate test and fine-grained test wall of Saccamminid sp. 24 is somewhat reminiscent of *Conqueria*, but the wide aperture persuades us not to refer it to this genus.

Distribution. Saccamminid sp. 24 is found in the Yalta region of the Black Sea (depth 87 m) in silty sediment with dead *Phaseolina* shells.

Saccamminid sp. 25 (Anikeeva et al., 2019)

(Fig. 5.32)

Description. The test is broadly spindle-shaped, 230 μm long and 133 μm wide with a coefficient C of 1.7. Two apertures (diameters 18 μm and 13 μm) are situated at the ends of the test (Fig. 5.32). The wall is finely agglutinated and translucent. The cell body completely fill the test interior and contains numerous clear mineral particles, small diatoms and vacuole-like features.



Figure 5.32. Saccamminid sp. 25 (Scale bar: 50 μm)

Differential diagnosis. This species is somewhat similar to Allogromiid sp. E (Sergeeva & Anikeeva, 2006, Fig. 12; Sergeeva et al., 2010, Pl. 4, Fig. A) in the general shape of the test and the presence of two terminal apertures. It differs in the form of apertures and the contents of the cytoplasm.

Distribution. The species is found at 61-87 m depth in the Yalta region of the Black Sea (South Crimea shelf) in silty sediment with dead *Phaseolina* shells and in sediment with stony rubble overlain by red silt.

Saccamminid sp. 26 (Anikeeva et al., 2019)

(Fig. 5.33)

Description. The test is ovoid in outline, 340 μm long and 200 μm wide with a coefficient *C* of 1.7. There is a single rounded aperture (diameter 36 μm) at one end. The wall is dense, translucent, and finely and evenly agglutinated (Fig. 5.33). The cell body is separated by a fairly wide space from the test wall.

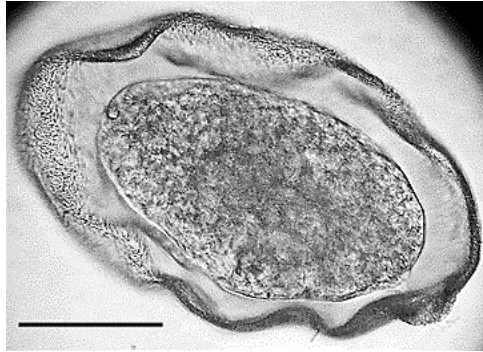


Figure 5.33. Saccamminid sp. 26 (Scale bar: 100 μm)

Differential diagnosis. This species is somewhat similar to Allogromiid sp. N of Sergeeva et al., (2010; Pl. 2, Fig. C) in the shape of the test and large space between the test wall and the cell body. However, the thickness of the wall and shape of aperture are different in the two species.

Distribution. The species is found in the Yalta region of the Black Sea (South Crimea shelf) at 87 m depth on silty sediment with dead *Phaseolina* shells.

Saccamminid sp. 27 (Anikeeva & Gooday, 2016; Anikeeva et al., 2019)

(Fig. 5.34)

Description. Small oval test, measuring 245 x 168 μm with a coefficient *C* of 1.4. The agglutinated wall is thick (Fig. 5.34). The aperture is a simple round hole, about 23 μm in diameter, located at the slightly narrower end of the test. The cytoplasm is heterogeneous, although details are obscured by the thickness of the wall.

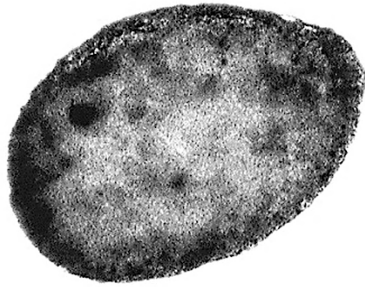


Figure 5.34. Saccamminid sp. 27 (Scale bar: 100 μm)

Differential diagnosis. Saccamminid sp. 27 has similarities with Allogromiid sp. E in terms of shape and size of the test, but differs from it in the structure of the test wall and the number of apertures.

Distribution. The species occurs in the area of Zernov's *Phyllophora* field (NW Black Sea) at a depth of 38 m in silt with a broken mollusc shells. It was also found on the Feodosiya shelf and in the Kalamitsky Gulf at a depth of 36-50 m in black silt with fragments of mollusc shells.

Saccamminid sp. 28

(Fig. 5.35)

Description. The test ranges from oval to slightly elongated (Fig. 5.35A, B), and from 400 x 165 μm to 420 x 250 μm in size, with a coefficient *C* between 1.7 and 2.4. The aperture is a simple round hole with a diameter of 26-31 μm located at one of the ends of the test. The wall is dense and thick. The cytoplasm is homogeneous and separated from the test wall by clear space. A nucleus with a diameter of 65 μm is located centrally.

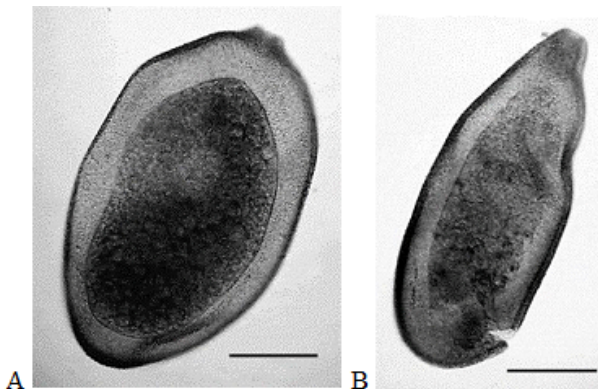


Figure 5.35. Saccamminid sp. 28: A, B—general view of two different specimens (Scale bar: 100 μm).

Differential diagnosis. Morphologically, this species is closest to Saccamminid sp. 8 and Saccamminid sp. C. However, it lacks the capsule-like aperture characteristic of Saccamminid sp. 8, and is distinguished from Saccamminid sp. C by the presence of one rather than two apertures.

Distribution. The species is found in the area of the Zernov's *Phyllophora* Field (NW Black Sea) at a depth of 24 m in the silty sand with mollusc shell fragments.

Saccamminid sp. 29

(Fig. 5.36)

Description. The test is large, measuring 657 x 130 μm with a coefficient *C* of around 5. It is elongated, slightly expanding towards the apertural end (Fig. 5.36). The aperture is a simple round hole with a diameter of 50 μm , located at the wider end of the test. The wall is dense and thick. The cytoplasm is heterogeneous, although the details cannot be seen clearly through the wall.



Figure 5. 36. Saccamminid sp. 29 (Scale bar: 100 μm)

Differential diagnosis. Saccamminid sp. 29 is similar to *Conqueria* in terms of the test shape and location of the aperture, but it has a much denser and thicker test wall and lacks an apertural neck.

Distribution. The species is found on the north-western shelf of the Crimea at a depth of 84 m in the biotope of *Phaseolina* silt.

Saccamminid sp. 30

(Fig. 5.37)

Description. The test is large, measuring 745 x 300 μm , with a coefficient *C* of about 2.5. It is elongated and spindle-shaped (Fig. 5.37). Two apertures with a diameter of about 90 μm are symmetrically located at the opposite ends of the test. The agglutinated wall is very dense and thick, completely obscuring the cytoplasm.

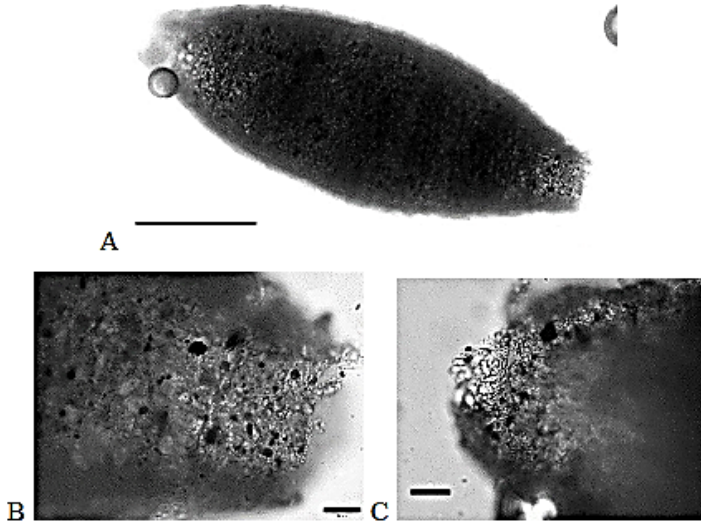


Figure 5.37. Saccamminid sp. 30: A – general view, B, C – apertures. (Scale bar: A – 200 μm , B, C – 20 μm)

Differential diagnosis. Saccamminid sp. 30 resembles *Krymia fusiformis* in the form of the test and the location of the apertures, but differs in its larger size, thicker, opaque wall and lack of apertural necks.

Distribution. This species is found in the Sea of Azov at a depth of 6 m in silty sand with fragments of mollusc shells.

Saccamminid sp. 31

(Fig. 5.38)

Description. The test is elongated, measuring 430 x 95 μm , with a coefficient *C* of about 4.5 (Fig. 5.38). The aperture, approximately 20 μm in diameter, is located on a relatively long neck (length \approx 60 μm) at the narrower end of the test. The wall is thick and agglutinated. The cytoplasm is obscured by the test wall.

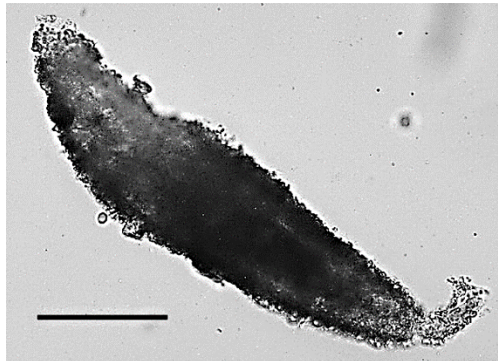


Figure 5.38. Saccamminid sp. 31. (Scale bar 100 μm).

Differential diagnosis. Saccamminid sp. 31 is similar to species of the genus *Vellaria* in the shape of an aperture neck, but differs from them in the shape of the test, the larger size and the thick agglutinated, almost opaque test wall.

Distribution. This species was found at a depth of 252 m in the anoxic zone near the Istanbul Strait (Bosporus). The sediment was black silt with a strong smell of hydrogen sulphide.

Saccamminid sp. 32

(Fig. 5.39)

Description. The test is large, measuring 600 x 220 μm , with a coefficient *C* of about 2.7. It is elongated, and spindle-shaped (Fig. 5.39A), The aperture, about 45 μm in diameter, is located at the slightly pointed end of the cell (Fig. 5.39B). The agglutinated wall is thick but fragile. The cytoplasm cannot be seen clearly, although a large number of rounded transparent inclusions, ranging in diameter from 17 to 45 μm , are visible in some places (Fig. 5.39C).

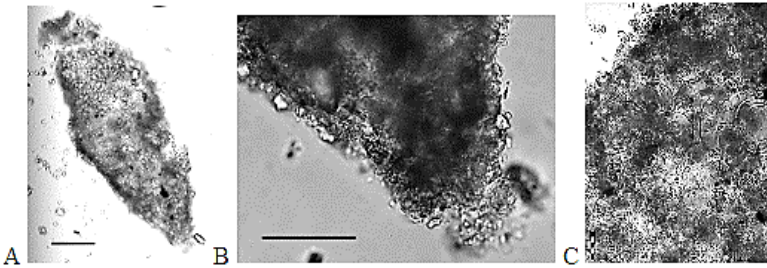


Figure 5.39. Saccamminid sp. 32. A – general view, B – aperture, C – protoplasm with rounded transparent inclusions (Scale bar: A – 100 μm ; B – 50 μm)

Differential diagnosis. Saccamminid sp. 32 resembles Saccamminid sp. 31 in the appearance of the test wall and the elongate shape. The main difference is the larger size of the test and the absence of an apertural neck in Saccamminid sp. 32.

Distribution. This species was found at a depth of 252 m in the anoxic zone near the Istanbul Strait (Bosporus). The sediment was black silt with a strong smell of hydrogen sulphide.

Order Allogromiida Loeblich & Tappan, 1961

Family Allogromiidae Rhumbler, 1904.

Subfamily Argillotubinae Avnimelech, 1952

Genus *Goodayia* Sergeeva & Anikeeva, 2008

Diagnosis of genus: Test 210–465 μm long and 50–150 μm wide, with a thin, flexible wall. It is elongate and expands in width from the middle to the apertural end. The test wall has two transparent proteinaceous membranes, and the cytoplasm is more or less separated from the inner layer of the wall. The cytoplasm is finely granular, homogeneous, usually without foreign inclusions. The single terminal apertural structure has an asymmetrical, beak-like shape with apertural opening under beak. A single nucleus is situated more or less in the middle of the test.

Goodayia rostellata Sergeeva & Anikeeva, 2008

[Syn. *Allogromiidae* gen. sp. B, (Sergeeva & Anikeeva, 2006)].

(Fig. 5.40)

Description. Test monothalamous, elongate, length 210-310 μm , width 80-150 μm , widening from the middle to the aperture end (Fig. 5.40A, B). The single aperture is located asymmetrically and associated with a beak-shaped structure. The wall is flexible, composed of organic material and has a two-layered structure. The finely granulated, homogeneous cytoplasm lacks foreign inclusions and is separated from the test wall by a more or less clear space. The nucleus is usually close to the middle of the test, less often near the aperture, and about 23 μm in diameter.

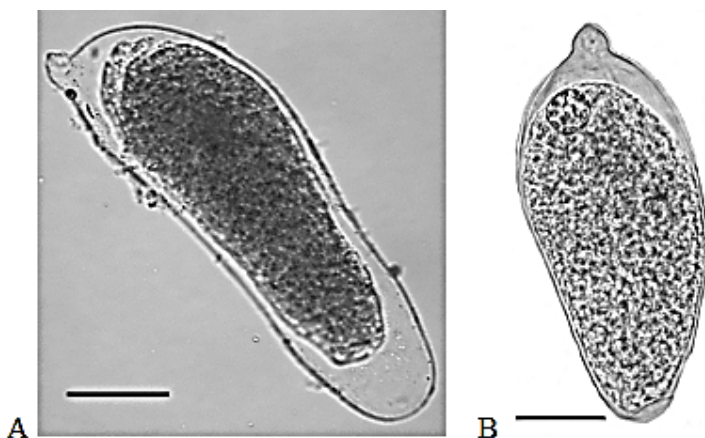


Figure 5.40. *Goodayia rostellata*. A, B – general view of two specimens (Scale bar: 50 μm)

Differential diagnosis. In terms of test size and shape, the double-layered construction of the wall, and the presence of a single terminal aperture, *Goodayia* resembles *Gloiogullmia* Nyholm, 1974. However, there are significant differences between the two genera. In contrast to *Gloiogullmia*, the wall of *Goodayia* is clean and devoid of adhering foreign mineral or organic particles and the cytoplasm is homogeneous, without exotic inclusions. The most notable difference, however, is the presence of a wide, fairly simple aperture in *Gloiogullmia* compared to the relatively small aperture hidden under a beak-shape apertural structure in the new genus.

The shape and size of the test of *Goodayia* is also rather similar to that of allogromiids in the genus *Rhynchogromia* Rhumbler, 1894. In both cases, there is also one aperture and a single nucleus. However, specimens of *Rhynchogromia* commonly occur in the empty tests of other foraminifers. In addition, the test wall comprises a single layer that incorporates numerous plate-like or elongate secreted bodies, compared to the clear, transparent wall of *Goodayia*.

Distribution. *Goodayia rostellata* is an eurybiont species, that inhabits a wide range of water depths as well as different regions of the Black Sea. It occurs both in coastal sediments (4–19 m depth) of the Sevastopol area (Kazach'ya, Kruglaya, Balaklavskaya, Uchkuevka, Laspi Bays), as well as on the Crimean, Caucasian and Bulgarian shelves across a depth range of 105–160 m water depth. The oxygen

concentration on the Crimean shelf decreased with increasing depth, whereas the sulfide concentration started to increase below 157 m (Sergeeva et al., 2008). *Goodyia rostellata* inhabits biotopes ranging from fine-granular sands to fine silts.

Genus *Micrometula* Nyholm, 1952

Diagnosis of genus: The test is elongate, from 0.7 to 1.2 mm in length and gradually narrowing at both ends. The wall is organic, hyaline, non-perforated, with fine longitudinal surface grooves; one rounded aperture is located at the larger end of the test, but some specimens also have a second, temporary aperture in the form of a small hole at the opposite end of the cell; one nucleus.

***Micrometula* sp.**

(Fig. 5.41)

Description. The test has the tapered, elongated shape that is typical for representatives of this genus (Fig. 5.41A). The length is 500 μm and the maximum width 60 μm , with a coefficient *C* of approximately 8.3. The single aperture is located on a short neck, measuring 28 x 34 μm , located at the wider end of the test (Fig. 5.41B). The test wall is organic, transparent, without visible agglutination. The cytoplasm fills the test almost completely. The nucleus (36 μm in diameter), is positioned closer to the apertural end.

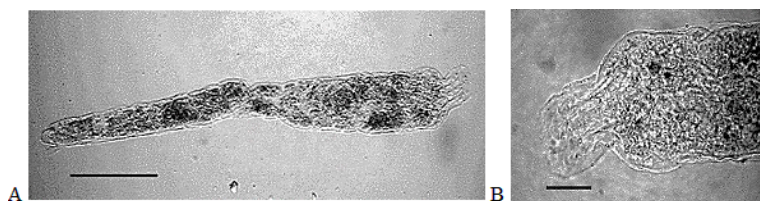


Figure 5.41. *Micrometula* sp. A – general view, B – aperture; (Scale bar: A – 100 μm , B – 20 μm)

Differential diagnosis. This represents the first record of *Micrometula* from the Black Sea. Morphologically, the closest species to *Micrometula* sp. is *Vellaria* sp. C. The two species differ in the shape and structure of the aperture neck, as well as in the shape of the test.

Distribution. This species is found in the southwestern region of the Crimean shelf at a depth of 155 m in bottom water and detritus.

Species with some resemblance to *Nodellum* Rhumbler, 1913

The following species have some slight superficial resemblance to *Nodellum* in terms of test shape, but they lack the thick, brownish test wall of this distinctive deep-sea genus. *Nodellum* occurs in the Mediterranean but is currently unknown in the Black Sea.

***Nodellum*-like form 3** (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.42)

Description. The test is elongated, 365 μm long, 60 μm wide, with a coefficient *C* of about 6 (Fig. 5.42). The single aperture is a barely visible inner canal. At the aperture end, the test is slightly narrowed to form a second segment. The wall is organic and very thin. The cytoplasm is homogeneous, granular, with some space remaining between the cell body and the test wall.



Figure 5.42. *Nodellum*-like form 3 (Scale bar: 50 μm)

Differential diagnosis. This species resembles typical members of *Nodellum* only in terms of the overall test shape. In particular, the test is much smaller and the wall is very different from the relatively thick, brownish wall that characterizes this genus.

Distribution. This species is found in the NW of the Black Sea at a depth of 150 m in silty sand with bivalve shell fragments.

***Nodellum*-like form 5** (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.43)

Description. The test is elongate, length 205 μm , width 35 μm , coefficient *C* 5.8. The aperture is rather wide (about 17 μm). There is a slight narrowing at the proximal end that defines an initial segment that can be compared to a proloculus. (Fig. 5.43). The wall is smooth and in some places slightly agglutinated. The cytoplasm is homogeneous, granular, and fills the intracellular space completely.

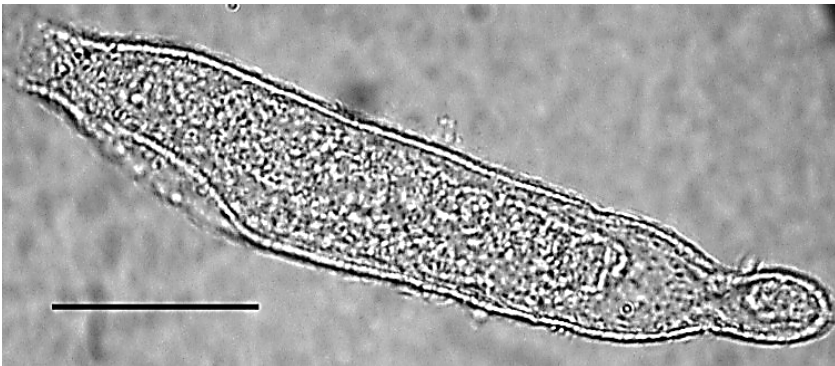


Figure 5.43. *Nodellum*-like form 5 (Scale bar: 50 μm)

Differential diagnosis. As the *Nodellum*-like form 3, this species resembles typical members of *Nodellum* only in terms of the overall test shape. In particular, the test is much smaller and the wall is very different from the relatively thick, brownish wall that characterizes this genus.

Distribution. This species is found in the NW of the Black Sea at a depth of 150 m in silty sand with broken bivalve shells.

***Nodellum*-like form 6** (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.44)

Description. The test is larger and wider than the two other species assigned to this grouping, and has some minor constrictions; length 445 μm , width 160 μm , coefficient *C* 2.8. (Fig. 5.44). The aperture is 56 μm wide. The wall is thin, transparent, and composed of organic material without agglutination. The cytoplasm is homogeneous, except for a few mineral particles.

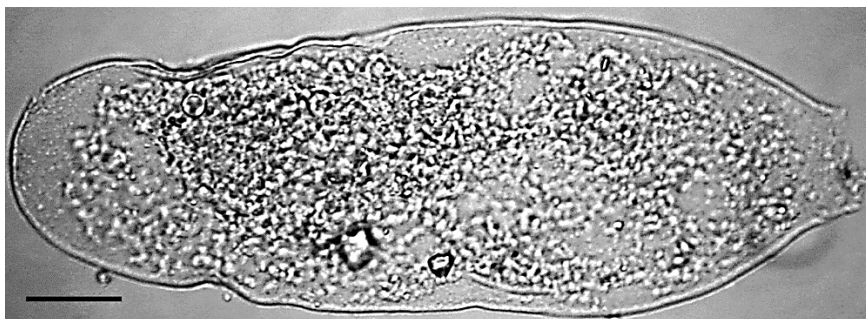


Figure 5.44. *Nodellum*-like form 6 (Scale bar: 50 μm)

Differential diagnosis. In terms of the aperture structure and the presence of a small narrowing at the proximal end of the test, this species resembles the previous one (*Nodellum*-like form 5), but the test is much longer and wider.

Distribution. This species is found in the NW of the Black Sea at a depth of 150 m in silty sand with broken bivalve shells.

Subfamily Shephardellinae Loeblich & Tappan, 1984

Genus *Krymia* Anikeeva, Sergeeva & Gooday 2013

Diagnosis of genus: Test monothalamous, 310–470 μm long, 70–100 μm wide, coefficient *C* 3.9–5.4 (typically ~4.5). Elongate and spindle-shaped with two terminal apertures situated on narrow neck-like extensions of the test. Wall is flexible, semi-transparent, non-reflective, composed of organic layer overlain by fine agglutinated particles. Cytoplasm is finely granular but with various inclusions, typically including long, needle-like spicular structures.

Krymia fusiformis Anikeeva, Sergeeva & Gooday 2013

[Syn.: *Saccamminidae* gen. sp. A] (Sergeeva & Anikeeva, 2006)

(Fig. 5.45)

Description. The test is elongate, average length 397 μm and width 110 μm , with a coefficient *C* of about 3.6. It is spindle-shaped (Fig. 5.45A, B), smoothly tapering to the ends where tubular apertural structures (up to 28 μm long) are located (Fig. 5.45C). The test wall is flexible, translucent, grayish with a granular texture and composed of small mineral grains. In most individuals, the cytoplasm contains long inclusions that occupy the entire length of the test (Fig. 5.45A). The diameter of the nucleus is 16.8 μm .

Differential diagnosis. *Krymia* is most similar to *Phainogullmia* Nyholm 1955 in terms of the elongate form of the test and the presence of terminal apertures. The test is more clearly tapered towards either end in the new genus, but the most striking difference is in the composition and appearance of the test wall. This is opaque, yellowish-brown in color with a shiny reflection in *Phainogullmia* (Nyholm, 1955a) but semi-transparent and nonreflective in the new genus. Another agglutinated monothalamous genus with an elongate test, *Conqueria* Gooday and Pawlowski, 2004, has a more cylindrical form and only one aperture.

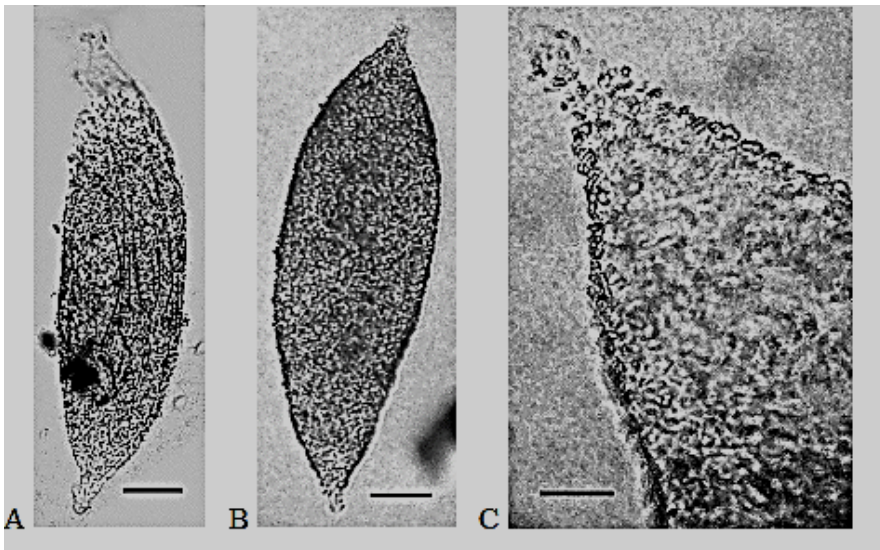


Figure 5.45. *Krymia fusiformis*. A, B – general view of two different specimens, C – the apertural end (Scale bar: A, B – 50 μm , C – 20 μm)

Distribution. *Krymia fusiformis* is found in the northwestern part of the Black Sea, in Kazachya Bay (Sevastopol region) in fine sand at shallow depths (10-17 m), as well as near Yalta, Karadag and Feodosia (southern shelf of Crimea) across the depth range 20-55 m in sandy and silt bottom sediments.

Genus *Nemogullmia* Nyholm, 1953

Diagnosis of genus: Test free or may inhabit empty foraminiferal tests or worm tubes, elongate, straight, or convoluted, 1.6 mm to 19.0 mm in length; wall smooth, transparent, whitish to pale red, may have some agglutinated material; intermittent constrictions may occur; temporary small apertures developed at ends of the test; cytoplasm opaque, containing oil droplets, one or more nuclei, pseudopodia reticulose; sexual reproduction with biflagellate gametes that develop within test of uninucleate gamont following temporary closure of apertures; schizont multinucleate, reproducing by fission. (After Loeblich and Tappan, 1988).

Nemogullmia pontica Sergeeva & Anikeeva, 2020

(Fig. 5.46)

Description. The test is free, monothalamous, elongated and worm-shaped (Fig. 5.46 A). The test may exhibit several constrictions (Fig. 5.46 D). The length varies from 730 to 1800 μm , width from 26 to 62 μm , and the coefficient *C* from 28-40 to 41-69, depending on the total length. Two identical apertures are symmetrically located at opposite ends of the test (Fig. 5.46 B, C) and are represented by rounded holes at the ends of tubular necks, the sizes of which vary from 32 x 10 μm to 52 x 24 μm . In some individuals, the dimensions of the apertures may vary slightly. The test wall is transparent, flexible, organic. The cytoplasm is homogeneous, granular, with a large, oval, slightly elongated nucleus, measuring 30 x 12 μm , located towards the centre of the cell body.

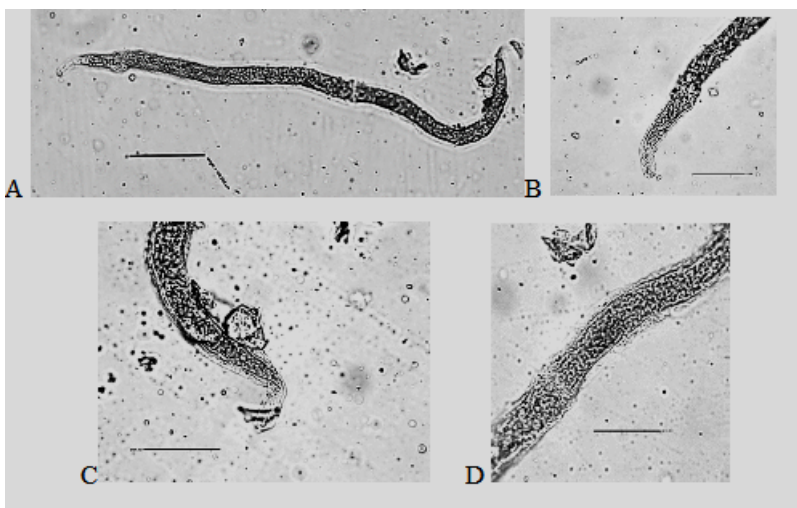


Figure 5.46. *Nemogullmia pontica*: A – general view, B, C – the apertures, D – nucleus (Scale bar: A – 100 μm ; B, C, D – 50 μm).

Differential diagnosis. Based on the shape of the test, the number, structure and arrangement of the apertures and the general appearance of the cell, we attributed this species to the genus *Nemogullmia*. It differs from the genus *Marenda* Nyholm, 1951, in the smaller size of the test, as well as the obvious apertural structures. At the same

time, in terms of shape and size of the test, the structure of its wall and cytoplasm, and the presence of a large oval nucleus in the center of the cell, the new species is similar to *Shepherdella taeniformis* Siddall, 1880. Since the studied specimens were fixed with alcohol, it is not known whether living individuals had a yellow cytoplasm like *S. taeniformis*. The main difference between *Nemogullmia pontica* and *S. taeniformis* consists in the presence of longer aperture necks in the studied species. Unfortunately, we do not have any living material that can more accurately confirm the identification of the species, but at this stage of the study it is most convenient to assign it to the genus *Nemogullmia*.

Distribution. The species was found in the Kerch Strait, where it is associated with methane seeps at a depth of 90 m, in the area of the Istanbul Strait (Bosporus) at a depth of 252 m in black pelite silt with a strong smell of hydrogen sulfide and a large number of clusters of fungal filaments and bacterial mats, and in the Karkinitzky Gulf near Cape Tarkhankut (NW) at a depth of 30 m in sandy silt with a small amount of mollusc shell fragments and live molluscs.

***Nemogullmia longissima* Sergeeva & Anikeeva, 2020**

(Fig. 5.47)

Description. The test is free, monothalamous, very elongate and thread-like in shape (Fig. 5.47A). The length and width vary from 1470 x 15 μm to 3200 x 32 μm ; coefficient *C* varies from 50 to 100 and from 100 to 177, depending on the length of the body. Apertures are located on opposite ends of the test on long necks (Fig. 5.47B). The wall is organic, transparent, thin, elastic. The protoplasm is separated from the test wall by a distinct space varying in width along the length of the test, probably the result of preservation in ethanol. A large elongated oval nucleus, about 50 μm in diameter (Fig. 5.47 C, D), is located in the central part of the cell.



Figure 5.47. *Nemogullmia longissima*: A – general view, B – the apertures, C – nucleus (Scale bar: A – 200 μm ; B, C – 20 μm).

Differential diagnosis. *Nemogullmia longissima* is much longer than *N. pontica* (1000-3200 μm compared to 730-1800 μm), narrower width and substantially larger (3 times or more) coefficient *C*. Due to this extreme length, the test of *Nemogullmia longissima* is much more flexible and fragile than that of *Nemogullmia pontica*.

Distribution. The species is found in the Black Sea in the Kerch Strait in the area of methane seeps at a depth of 79-90 m in pelite silt with a live *Phaseolina* and a broken mollusc shells.

Nemogullmia bosphorica Sergeeva & Anikeeva, 2020

(Fig. 5.48)

Description. Test monothalamous, elongate and worm-shaped, measuring 960 to 1100 μm in length (Fig. 5.48A). The width is fairly constant ($\sim 40\text{-}50\ \mu\text{m}$) throughout the body, but tapers smoothly at both ends, which have two identical apertures on small necks, measuring $11 \times 9\ \mu\text{m}$ and $14 \times 11\ \mu\text{m}$ (Fig. 5.48B, C). The wall is organic, flexible, elastic and transparent. The cytoplasm is separated from the cell wall by a distinct space and contains 6 - 11 nuclei with a diameter of $17\text{-}19\ \mu\text{m}$ distributed along the entire cell body (Fig. 5.48D).

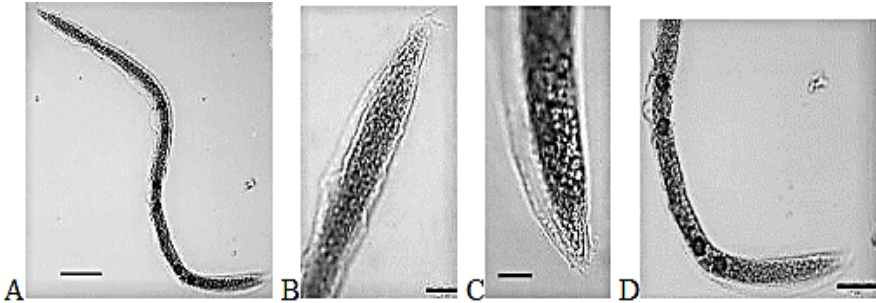


Figure 5.48. *Nemogullmia bosphorica*: A – general view, B, C – apertures, D – nuclei (Scale bar: A – 200 μm ; B, C – 20 μm ; D – 50 μm)

Differential diagnosis. *Nemogullmia bosphorica* differs from *Nemogullmia longevariabilis* Nyholm, 1956 in the absence of agglutinating detritus adhering to the test wall and the ordered arrangement of the smaller nuclei.

Distribution. *Nemogullmia bosphorica* is found in the area of the Istanbul Strait (Bosporus) at depths of 82-135 m under normoxic and hypoxic conditions in dense silt with mollusc shells.

Genus *Tinogullmia* Nyholm, 1954

Diagnosis of genus: The test is oblong, tubular, tapering to both ends. The wall of the test is vitreous, protein, non-perforated. Apertures are located on narrow tubular necks of the same size, which are on opposite ends of the test. Cytoplasm is mainly free of detritus particles. Pseudopodias are straight, thin and very brittle. The nucleus is rounded, large. Living individuals occupy a horizontal position in bottom sediments (adapted from Loeblich and Tappan, 1987).

Tinogullmia lukyanovae Gooday, Anikeeva & Sergeeva, 2006

(Fig. 5.49)

Description. The test is 220 - 550 μm long and 120 - 160 μm wide with a coefficient *C* varying from 1.8 to 3.2. The lateral outline is rather variable, ranging from oval to spindle-shaped to cylindrical, and the cross-section is more or less circular. Identical terminal apertures are located at the ends of rounded or more elongated, nipple-like projections (Fig. 5.49). The test wall is organic, the surface smooth but not clearly reflective. The cytoplasm is yellowish-brown and finely granular without a visible nucleus.

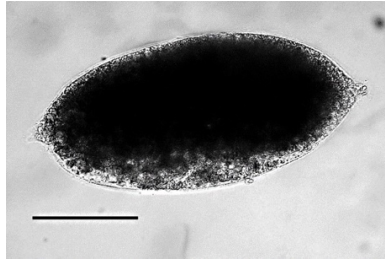


Figure 5.49. *Tinogullmia lukyanovae* (Scale bar: 100 μm)

Differential diagnosis. *T. lukyanovae* has a much wider test than the type species *T. hyalina*, and much shorter aperture necks.

Distribution. Despite its low abundance, the species is widely distributed in all investigated water areas of the Black Sea across a wide range of depths in conditions ranging from normoxic to anoxic with hydrogen sulfide (3-250 m). It is found in sandy mud with an admixture of shells, in fine silty sand, siltstone and pelite black silts.

Tinogullmia cf. riemanni (Sergeeva, Anikeeva & Gooday, 2010)
(Fig. 5.50)

Description. The test is elongated and curved (Fig. 5.50 A), length 130 - 230 μm , width 30 - 60 μm , coefficient *C* 3.8 - 4.3. Apertures are located at the ends of necks, measuring about 10 x 14 μm , situated at opposite ends of the test (Fig. 5.50 B, C). The wall is organic, thin, without agglutination. The cytoplasm is homogeneous, sometimes containing large vacuole-like inclusions.

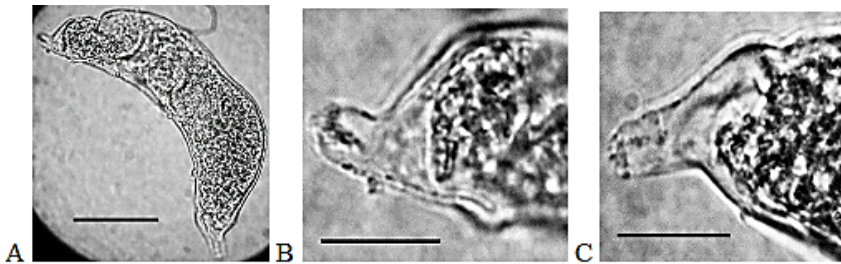


Figure 5.50 *Tinogullmia cf. riemanni*. A – general view, B, C – apertures (Scale bar: A – 50 μm ; B, C – 20 μm)

Differential diagnosis. The Black Sea representative of *Tinogullmia cf. riemanni* is similar to the typical species *T. riemanni*, found at bathyal and abyssal depths, in key morphological features, namely convex-concave shape of the test, body size, and the shape and location of the apertures.

Distribution. The species is found in the Black Sea in the depth range of 130-150 m in *Phaseolina* silt as well as in silty sand with admixture of bivalve shell fragments.

***Tinogullmia* sp. 1** (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.51)

Description. As in the case of other tinogullmiids, the elongate test tapers towards the ends (Fig. 5.51A, B), which are drawn out into tubular apertural structures (Fig. 5.51C, D). The average test length is 240 μm , the width is 70 μm and the coefficient *C* is 3.4; the apertural structures are 11 μm long and 8 μm wide. The test wall is transparent and organic, without agglutination. The nucleus is large (33 μm diameter) and situated more or less centrally.

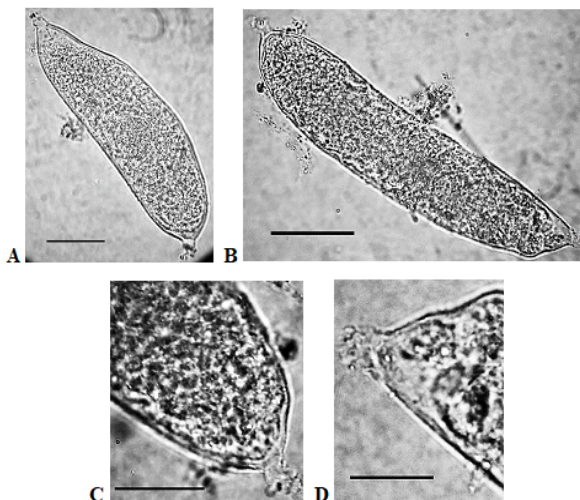


Figure 5.51. *Tinogullmia* sp. 1. A, B – general view of two different specimens, C, D – apertures (Scale bar: A, B – 50 μm ; C, D – 20 μm)

Differential diagnosis. Of the three undescribed species of *Tinogullmia* that we recognise, this one most closely resembles *T. lukyanovae* in the test form, the location of the apertural structures, and the homogeneity of the cytoplasm. However, differences in the apertural structures preclude a firm identification as *T. lukyanovae*.

Distribution. The species is found in the NW part of the Black Sea at a depth of 150 m in silty sand with an admixture of bivalve mollusc shells.

***Tinogullmia* sp. 2** [Syn. *Tinogullmia* sp. (Sergeeva, Anikeeva & Gooday, 2005)].

(Fig. 5.52)

Description. The test is organic, elongate, and slightly curved. The length varies from 250 to 1200 μm , the width from 40 to 140 μm and coefficient *C* varies from 5.4 for smaller specimens to 8.5 for larger ones. There are two symmetrically arranged terminal apertures on elongated necks with lengths of 17-40 μm for specimen 250-550 μm long and 55-80 μm for those 1200 μm long (Fig. 5.52A, B). The cytoplasm is finely granular, without an obvious nucleus.

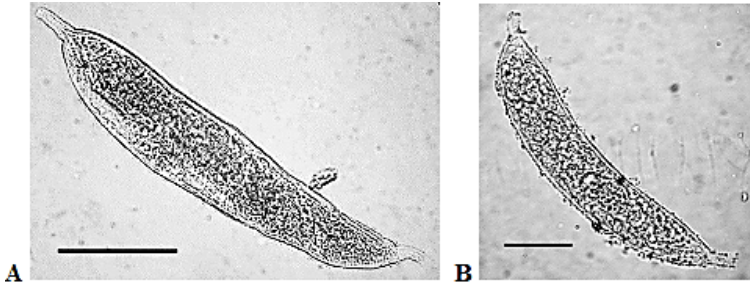


Figure 5.52. *Tinogullmia* sp. 2. A, B – general view of two different specimens (Scale bar: A – 100 μm , B – 50 μm)

Differential diagnosis. This species is similar to *T. hyalina*, except for the relatively wider test and the larger size range.

Distribution. Several individuals of this species have been found in the southwestern and northwestern parts of the Black Sea in areas of methane seeps at depths of 78 m in the *Phaseoline* silt biotope. In the area of the submarine Dnieper Canyon in the redox zone, the species was recorded at depths between 120 and 180 m on substrates of various types, ranging from detritus-rich to silty sand with an admixture of bivalve fragments. On the western shelf of the Crimea, it was found at depths of 83-104 m in the *Phaseolina* silt biotope.

***Tinogullmia* sp. 3** (Anikeeva et al., 2019)

(Fig. 5.53)

Description. The test is elongate, parallel-sided, cylindrical in shape, and measures 377 μm long, 80 μm wide with a coefficient *C* of 4.7 in the figured specimen (Fig. 5.53A). Two short, rather poorly defined aperture necks, each ~14 μm long, arise from the smoothly rounded ends of the test (Fig. 5.53B, C). The wall is organic, thin, transparent, without agglutinated particles. The cell body is finely granular and completely fills the test with no space intervening between it and the test wall.

Differential diagnosis. *Tinogullmia* sp. 3 is somewhat similar to *T. lukyanovae*, particularly regarding the test shape, but is much more elongate with longer aperture necks. As in the case of *T. lukyanovae* (Gooday et al., 2006), the placement of this species in the genus *Tinogullmia* is open to doubt. In contrast to the type species *T. hyalina*, and *Tinogullmia* sp. A of the present study, the cell body occupies the entire volume of the test, while the terminal apertural tubes are rather poorly defined and lack a central thread of cytoplasm. It seems likely that *Tinogullmia* sp. 3 and *T. lukyanovae* will eventually require the establishment of a new genus, although this would require genetic data from one or both species.

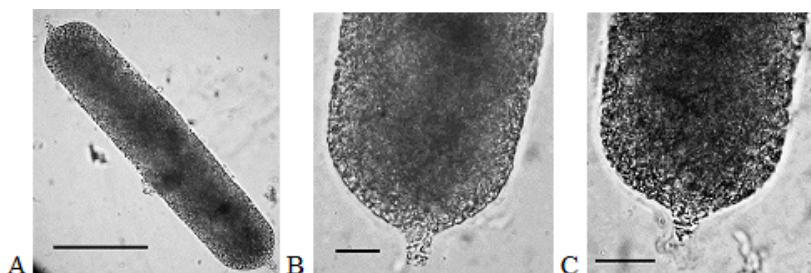


Figure 5.53. *Tinogullmia* sp. 3. A – general view, B, C – apertures (Scale bar: A – 100 μm , B, C – 20 μm)

Distribution. *Tinogullmia* sp. 3 was first discovered in shallow water in Kazach'ya Bay (Sevastopol region of the Black Sea) in 2003 (unpublished data) in silt with detritus and a small amount of sand. It also occurs in the Karkinitsky and Feodosiya Gulfs at depths of 19 and 50 m, where it is associated with silt mixed with a small amount of broken mollusc shells.

***Tinogullmia* sp. A** (Anikeeva et al., 2019)

(Fig. 5.54)

Description. Test elongate, somewhat lenticular in shape, length 220 μm , width 63 μm , coefficient C 3.5 in the figured specimen. Two terminal apertures are located at the ends of tubular necks, each ~ 22 μm long (Fig. 5.54). The wall is organic, thin, transparent, without agglutinating particles. The cell body is finely granular with a single nucleus and separated from the test wall by a distinct space. A fine thread of cytoplasm extends along the axis of the apertural tubes.

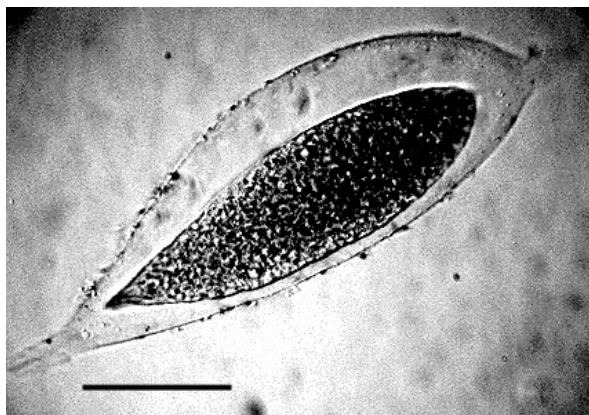


Figure 5.54. *Tinogullmia* sp. A (Scale bar: 50 μm)

Differential diagnosis. In comparison to the type species *Tinogullmia hyalina*, (e.g., Sergeeva et al., 2005), *Tinogullmia* sp. A has a less elongate test with a somewhat lenticular rather than cylindrical shape. However, the well-developed terminal tubular apertural necks, each with a central thread of cytoplasm, are features typical of the genus. The clear space between the test wall and the cell body is also observed in the

type species (although this space is particularly wide in the illustrated specimen and possibly exaggerated by artifactual effects). This mix of characters makes generic assignment somewhat problematic, but on balance, and in the absence of genetic data, we feel that a placement in *Tinogullmia* is the best option.

Tinogullmia sp. A differs from *T. lukyanovae* Gooday, Anikeeva & Sergeeva, 2006 (a species that may represent a distinct genus) in the shape of the test and in the presence of apertural necks that are typical for the genus. Three previously reported undescribed species from 120–180 m depth in the northwestern part of the Black Sea (Sergeeva et al., 2010), as well as *Tinogullmia* sp. 2 (Sergeeva and Anikeeva 2014, Pl.2, Figs. K1, K2), differ from *Tinogullmia* sp. A in some small details, notably the length and width of the apertural necks. The closest to this allogromiid species in terms of morphological features is the *Tinogullmia riemanni* Gooday, 1990. For the present, we regard our form as another distinct species. However, these Black Sea tinogullmid-like foraminifera require further morphological (and ideally genetic) analysis in order to determine whether they represent one or several species.

Distribution. This species is found in the Yalta area of the Black Sea at a depth 90 m in silty sediment with dead *Phaseolina* shells.

Genus *Bellarium* Anikeeva, Sergeeva & Gooday, 2013

Diagnosis of genus: Test monothalamous, rounded, slightly elongate to almost spherical with two terminal apertural necks, sometimes with dilated ends. Length, including apertural necks 250–655 μm , width 140–340 μm , coefficient *C* is about 1.7–2.0 (including apertural necks). Test wall thin, flexible, consisting of transparent organic material. Cytoplasm occupying entire test interior; generally, finely granular and homogeneous, but often with many vacuoles and foreign inclusions, including diatom frustules and metazoan remains. Nucleus small (20–80 μm) and usually not visible. (Adapted from Anikeeva et al., 2013).

Bellarium rotundum Anikeeva, Sergeeva & Gooday, 2013

[Syn. Allogromiidae gen. sp. D (Sergeeva & Anikeeva, 2006)]

(Fig. 5.55)

Description. The test is large, almost spherical, ranging in size from 250 to 620 μm (Fig. 5.55A, B). The average size of the test is 410 x 230 μm and the coefficient *C* varies from 1.7 to 2. Two relatively symmetrical apertures are located on long necks on the opposite sides of the test. The average length of the aperture neck is 50 μm , although in most individuals, one neck is 5–10 μm longer than the other. The wall is basically organic but in one of the illustrated specimens it is slightly agglutinated with finely dispersed material, whereas in the other specimen the agglutination is absent. The finely granulated cytoplasm contains various inclusions, rarely small mineral particles but more often diatom frustules. The diameter of the nucleus is about 30 μm .

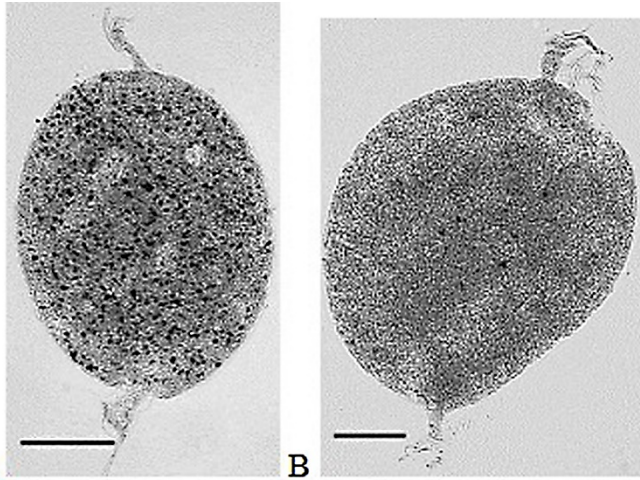


Figure 5.55. *Bellarium rotundum*. A, B – general view of two different specimens (Scale bar: 100 μm)

Differential diagnosis. The new species differs from *Tinogullmia lukyanovae*, also from coastal waters of the Black Sea (Gooday et al., 2006), in having a more compact, globular shape, generally longer apertural structures, and a thinner test wall. It is rather similar in overall morphology to some specimens of *Tinogullmia riemanni* from the deep NE Atlantic, but the organisation of the test and cytoplasm are quite different in the two species. In contrast to *B. rotundum*, there is a clear space between the cell body and test wall in *T. riemanni*. The apertural tubes are typically well defined with an axial thread of cytoplasm in *T. riemanni*, unlike the rather flimsy apertural structures of the new species.

Distribution. *Bellarium rotundum* inhabits shallow coastal habitats with sandy sediment near Sevastopol (Omega Bay, Uchkuevka-Lyubimovka region, 5-12 m depth), and the area of Zernov's *Phyllophora* field (24 m depth) in silty sand with mollusc shells. It was found also in a hypoxic area of the Sea of Azov (8-11 m depth).

Family Allogromiidae Rhumbler, 1904

Genus *Vellaria* Gooday & Fernando, 1992

Diagnosis of genus: The test is less than 1 mm long, symmetrically oval, with a thin organic wall, sometimes covered with a thin layer of fine agglutinating particles. The aperture is located at the end of a prominent apertural structure with an expanded termination. The cytoplasm is finely granulated, with one fairly large nucleus.

Vellaria pellucida Gooday & Fernando, 1992

(Fig. 5.56)

Description. Black Sea representatives of *V. pellucida* are similar to the type species first described for the Indian coast. The main features of the Black Sea specimens (shape of the test and the nature of its agglutination, form of the aperture) fully correspond to the features of type species (Fig. 5.56A, B). They vary from 140

to 420 μm in length, 78 to 186 μm in width, with a coefficient C ranging from 1.5 to 2.9. The thickness of the test wall is 7-10 μm . The nucleus is 12-28 μm in diameter.

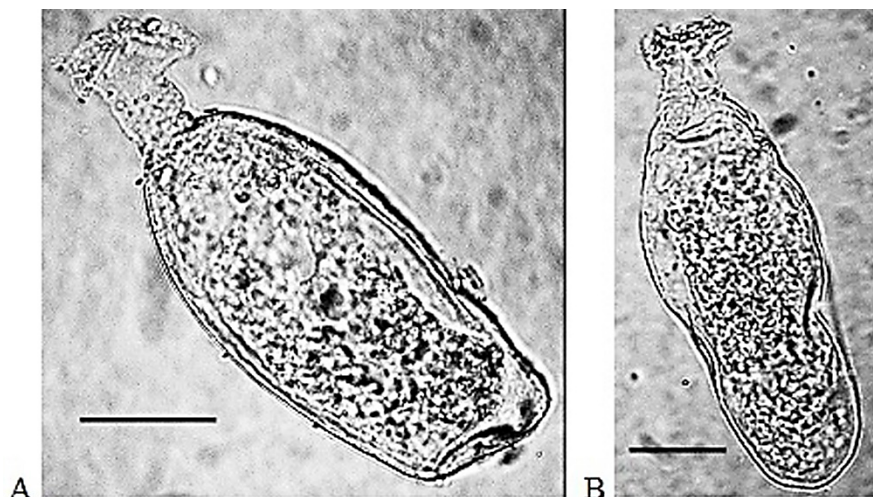


Figure 5.56. *Vellaria pellucida*. A, B - general view of two different specimens (Scale bar: 50 μm)

Differential diagnosis. The main difference between the Black Sea forms and the type species concerns the size of the nucleus: its diameter in the type species is more than 10 times that of the Black Sea form.

Distribution. The species is found in all the above-mentioned areas of the Black Sea at depths of 3 to 160 m. It is most often found in Uchkuevka - Lyubimovka area, Kazachya and Balaklava bays. The highest density of *V. pellucida* is observed in open coastal areas (48 thousands ind./m²) (Uchkuevka - Lyubimovka) in silt with admixture of mollusc shells, silty sand, fine and medium sand. It is also found on the Crimean shelf from the Karkinitsky Gulf to Cape Opuk, and in the area of the Zernov's *Phyllophora* field in silt with mollusc shell fragments. *V. pellucida* is also often found in the Sea of Azov.

Vellaria sacculus Gooday & Fernando, 1992

(Fig. 5.57)

Description. The test is oval and measures 240 x 130 μm on average, with a coefficient C of 1.9. The shape of the aperture is typical for the genus *Vellaria*. The walls have a thin veneer of finely agglutinated particles (Fig. 5.57A). The cytoplasm is homogeneous, granular (Fig. 5.57B) and the single nucleus is about 23 μm in diameter.

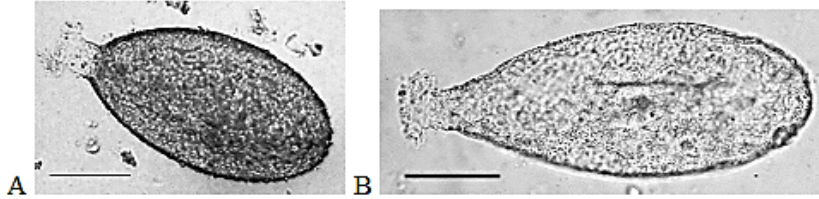


Figure 5.57. *Vellaria sacculus*. A, B – general view of two different specimens (Scale bar: 50 μm)

Differential diagnosis. *Vellaria sacculus* is smaller than *V. pellucida* and has a more rounded shape as well as a veneer of finely agglutinated material on the test surface.

Distribution. This species is found in the Black Sea at a depth of 3 to 22 m. The density at locations in Kazachya and Balaklava bays varies from 0.5 to 10.5 thousands ind./m². The sediments are sand with an admixture of mollusc shell fragments and detritus, pelite silt, polluted with oil and hydrocarbons and with a smell of hydrogen sulphide. *Vellaria sacculus* is found also in the Karkinitzky Gulf and in the area of the Zernov's *Phyllophora* field at a depth of 11-24 m in silty sand with admixture of mollusc shell fragments.

Vellaria solenta Sergeeva & Anikeeva, 2021
(Fig. 5.58)

Description. The test is elongate, and varies from 240 to 435 μm in length and 50 to 90 μm in width (Fig. 5.58A). The coefficient *C* (length/width ratio) varies from 3.4 to 7; on average it is about 5. The proximal end of the test is smoothly rounded in most specimens. The single aperture, diameter 18 to 26 μm , is located at the end of the elongated neck, situated at the narrower apertural end of the test. The apertural neck varies from funnel-shaped with a slightly ragged edge, as in typical representatives of the genus *Vellaria*, to cylindrical, sometimes becoming narrower at the end. In many individuals, the neck has short, thin processes that extend beyond the aperture (Fig. 5.58B). The wall is organic, thin, and flexible. A characteristic feature of the species is that the dense cytoplasm completely fills the test cavity and the apertural neck, adhering tightly to the test wall with no intervening space. The cytoplasm is fine-grained and generally homogenous, although with diatom frustules in some individuals. The nucleus (diameter 15–28 μm) is located in the distal (apertural) part of the cell but is not always visible.



Figure 5.58. *Vellaria solenta*, the holotype: A – general view of the specimen, B – apertural part (Scale bars: A – 100 μm , B – 20 μm)

Differential diagnosis. Three valid species belonging to the genus *Vellaria* are currently known: *V. pellucida* Gooday & Fernando, 1992, *V. sacculus* Gooday & Fernando, 1992 and *V. zuchellii* Sabbatini, Pawlowski, Gooday et Bowser, 2004. The first two species, first described from the Vellar estuary in SW India (Gooday and Fernando, 1992), occur in both the Black Sea (Sergeeva and Anikeeva, 2004; Anikeeva, 2007; Gooday et al., 2011; Anikeeva and Gooday, 2016) and the Sea of Azov (Sergeeva, 2016) quite frequently. The morphological similarity between the new species and the two Indian species is in the structure of the apertural neck and test wall. In *V. solenta*, the test is slightly more elongated than that of *V. pellucida* and *V. sacculus*. A distinctive feature of the new species is that the entire interior of the test and apertural neck is completely filled with cytoplasm. Also, the short, thin filaments that extend beyond the aperture in most individuals have not been observed in other species of the genus. *Vellaria solenta* resembles the Antarctic species *V. zuchellii* (Sabbatini et al., 2004) in the elongated shape of the test but new species differs in terms of the size of the test, the apertural structure and distribution of cytoplasm within the test.

Distribution. The new species was found in the Sivash Bay of the Sea of Azov at a depth of 5 to 10 cm, in muddy sediment with a hydrogen sulphide smell. The salinity was 74‰.

***Vellaria* with honeycombed cytoplasm**

(Fig. 5.59)

Description. The test is elongated, with an average size of 190 x 80 μm ; coefficient *C* of 2.4. The aperture, measuring 20-25 μm , is similar in shape to that of *Vellaria*. A distinctive feature of this species is the presence of numerous vacuoles in the cytoplasm, creating a honeycombe-like appearance (Fig. 5.59).



Figure 5.59. *Vellaria* with honeycombed cytoplasm (Scale bar: 50 μm)

Differential diagnosis. This species differs from *Vellaria pellucida* and *V. sacculus* in terms of the test shape and the honeycombed-like appearance of the cytoplasm. This Azov-Black Sea form has a less elongated test shape than the Antarctic species *V. zucchellii*, and also differs in the vacuolated appearance of the cytoplasm.

Distribution. This species inhabits both the Sea of Azov and some areas of the Black Sea, including the Caucasian region (unpublished data).

***Vellaria* sp. 1** (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.60)

Description. The test is oval in shape (Fig. 5.60), with an average test length of 306 μm , width of 106 μm , and coefficient *C* of 2.9. The apertural structure is 28 μm long and 32 μm wide. The wall is thin and composed of organic material. Cytoplasm is heterogeneous and contains small amounts of quartz particles.

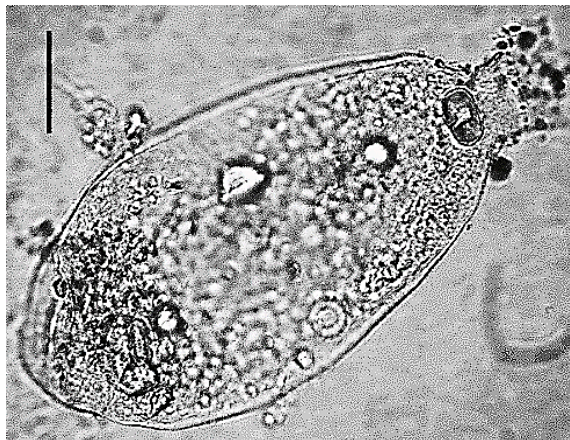


Figure 5.60. *Vellaria* sp. 1 (Scale bar: 50 μm)

Differential diagnosis. This species differs from *V. pellucida* and *V. sacculus* in the form of aperture, which resembles a trapezium. The "fringe" of the aperture is not

as pronounced as in these two other species. The apertural structure is wider, and not clearly distinct from the rest of the test.

Distribution. *Vellaria* sp. 1 is found in the NW Black Sea in the upper hydrogen sulfide border zone in a depth range from 150 to 180 m in detritus, silt with the addition of broken mollusc shells and in fine quartz sand.

***Vellaria*-like form** (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.61)

Description. The test is transparent, elongated, measuring 283 μm long, about 80 μm wide, coefficient *C* about 3.5 (Fig. 5.61A). There is a single prominent apertural extension, about 33 μm long (Fig. 5.61B). The cytoplasm is granular with a centrally situated nucleus.

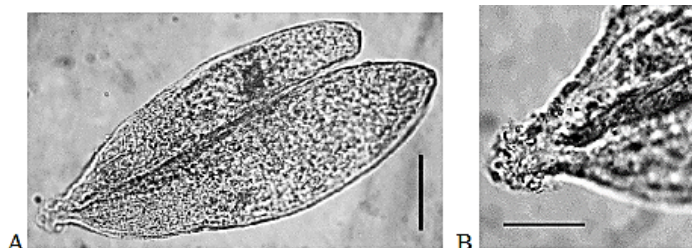


Figure 5.61. *Vellaria*-like form. A – general view of two specimens, B – aperture (Scale bar: 50 μm)

Differential diagnosis. "*Vellaria*-like form" differs from other representatives of *Vellaria* in having a narrower, more elongated test and a correspondingly narrower aperture.

Distribution. The species is found in the northwestern part of the Black Sea in the area of methane seeps at depths of 180 and 230 m in detritus-rich sediment.

***Vellaria* sp. C** (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.62)

Description. The test is elongate, (Fig. 5.62), approximately 400 μm long and 73 μm wide, with a coefficient *C* of 5.5. It has the flared apertural structure that is characteristic of the genus. The wall is organic, smooth and transparent. The cytoplasm is homogeneous, light yellow in color. The nucleus is clearly visible and has an average diameter of 20 μm .



Figure 5.62. *Vellaria* sp. C (Scale bar: 100 μm)

Differential diagnosis. *Vellaria* sp. C has a much more elongate test than *V. pellucidus* and *V. sacculus* and the shape and size of the test is different from that of other known species of the genus.

Distribution. The species is found in the north-western part of the Black Sea at depths of 150-180 m; in the south-western part of the Crimean shelf in the bottom water and detritus at a depth of 155 m; in the area of Yalta at a depth of 87 m in the silty sediments with dead *Phaseolina* shells. It is also found in the area of Sevastopol in shallow water (5-25 m) in sediment with dead molluscs shells and in fine silty sand with detritus.

***Vellaria* sp. 2**

(Fig. 5.63)

Description. The test is oval, measuring 274 x 120 μm with a coefficient *C* of about 2.3, and narrowing slightly at the aperture end (Fig. 5.63 A). The apertural structure is 36 x 20 μm in size and located on the narrower end of the test (Fig. 5.63B). The wall is organic, transparent, double-layered. The cytoplasm is granulated and contains vacuole-like inclusions. The diameter of the nucleus is about 17 μm .

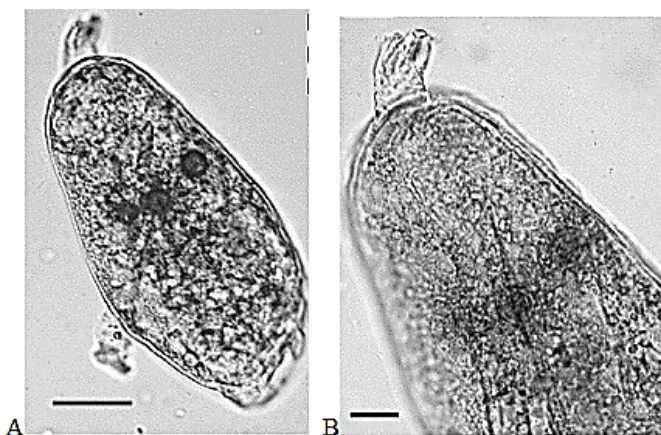


Figure 5.63. *Vellaria* sp. 2. A – general view, B – part with aperture (Scale bar: A – 50 μm , B – 20 μm)

Differential diagnosis. The shape and size of the test and the development of the aperture neck generally resemble those of *Vellaria*. However, the neck does not terminate in the fringed expansion that is typical of this genus.

Distribution. This species is found in the Sea of Azov at a depth of 6 m, in black silt with dead gastropod and ostracod shells and a distinct smell of hydrogen sulfide.

***Vellaria* sp. 3**

(Fig. 5.64)

Description. The test is of medium size, measuring 290 x 134 μm with a coefficient *C* of about 2.1, and is widest in front of the mid-point (Fig. 5.64A). The aperture is about 30 μm in diameter and located at the end of a thin neck with a somewhat expanded end that is situated on the wider end of the test (Fig. 5.64B). The wall of the test is thin, organic and transparent. The cytoplasm is finely granulated,

homogeneous, and entirely fills the test interior. There is a single nucleus with a diameter of about 50 μm .

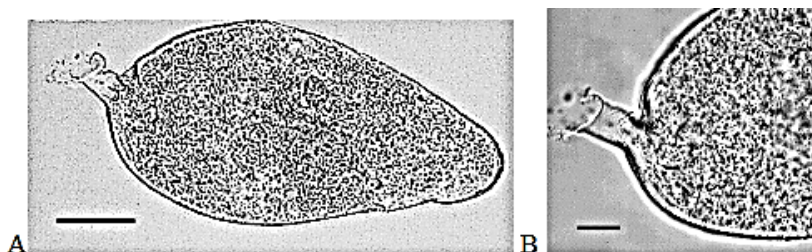


Figure 5.64. *Vellaria* sp. 3. A – general view, B – aperture’s part (Scale bar: A – 50 μm , B – 20 μm)

Differential diagnosis. The apertural neck of this species suggests a placement in *Vellaria*, although the neck is relatively thinner than that of typical species of the genus. The shape of the test, which is wider in the apertural half, is not typical.

Distribution. The species is found in the Sea of Azov at a depth of 8-10 m in black silt with detritus and a distinct smell of hydrogen sulfide.

***Vellaria* sp. X** (Anikeeva et al., 2019)

(Fig. 5.65)

Description. The test is elongate and 310 to 380 μm long; the figured specimen measures 350 x 91 μm with a coefficient C of 3.8. There is a flared, funnel-like apertural structure 29 μm long. The test wall is agglutinated, relatively thick, and there is a clear space between it and the cell body (Fig. 5.65). The diameter of the single nucleus is 28 μm .

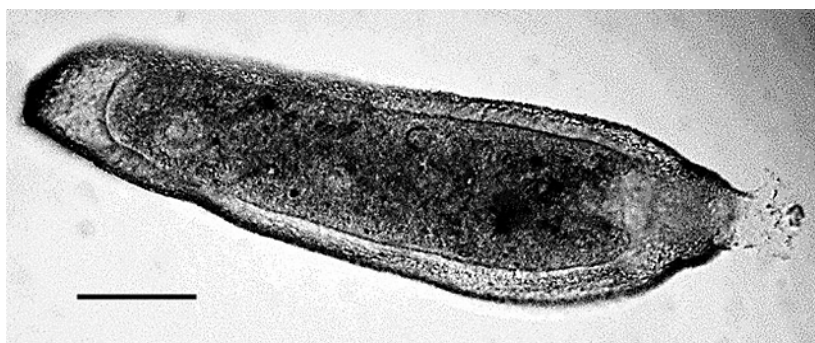


Figure 5.65. *Vellaria* sp. X (Scale bar: 50 μm)

Differential diagnosis. *Vellaria* sp. X has the flared apertural structure typical of this genus. It differs from other *Vellaria* species found in the Black Sea in having a thick agglutinated test wall, as well as being slightly larger with a much more elongated outline. In the latter respect it most closely resembles *V. zucchellii* of Sabbatini et al., (2004) from coastal waters of the Ross Sea (Antarctica). However, given the geographical separation between these Antarctic and Black Sea *Vellaria*,

and the lack of genetic data for our form, we hesitate to regard them as conspecific. As in the case of *Tinogullmia* and *Psammophaga* species, these Black Sea representatives of the genus *Vellaria* require further study in order to determine the taxonomic importance of the relatively minor morphological features used to distinguish them.

Distribution. The species is found in Yalta area at the depth 81 and 87 m in silty sediment with dead *Phaseolina* shells, and in the area near Kerch at a depth 95 m in the same kind of sediment.

Family Allogromiida *incertae sedis*

Genus *Bathyallogromia* Gooday et al., 2004a

Diagnosis of genus: The test is monothalamous, almost spherical, 140-450 μm in diameter. The single aperture is located in the center of a low, wide, protruding structure. The wall of the test is transparent, organic, smooth, without agglutinating particles. The cytoplasm contains various inclusions, among which mineral particles are often found. The color of the cytoplasm varies from light gray to greenish.

***Bathyallogromia* sp. 1** (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.66)

Description. The test is monothalamous, more or less spherical, measuring 450 x 400 μm with a coefficient *C* is about 1.1. The single aperture located in the centre of a low, broad projection measuring 20 μm wide and 10 μm high (Fig. 5.66). The cytoplasm occupies the entire test and contains various small inclusions. A peduncular sheath is clearly developed. A nucleus, 15 μm diameter, is located in the centre of the cell body.

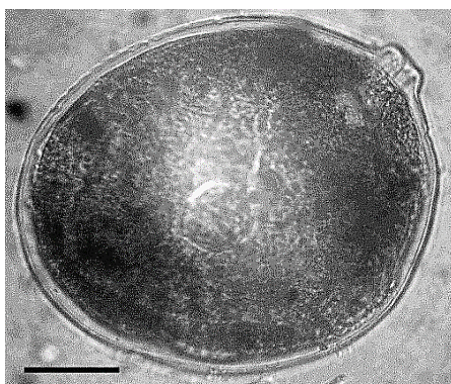


Figure 5.66. *Bathyallogromia* sp. 1 (Scale bar: 100 μm)

Differential diagnosis. This Black Sea species resembles *Bathyallogromia weddellensis* (Gooday et al., 2004a) from the Southern Ocean (1100-6300 m depth) in the form of the test, and the nature of the aperture. However, it lacks the large number of intracellular mineral inclusions present in the Antarctic species.

Distribution. The species is found in the north-western part of the Black Sea at a depth of 120-130 m in thin silt with an admixture of the broken *Phaseolina* shells.

***Bathyallogromia* sp. 2** (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.67)

Description. The morphological characteristics of this form are similar to those of *Bathyallogromia* sp. 1 and *B. weddellensis*. The test is almost spherical, measuring 500 x 430 μm , with a coefficient *C* of 1.1 (Fig. 5.67). The diameter of the aperture is about 50 μm . The test wall is organic, transparent, without agglutination.

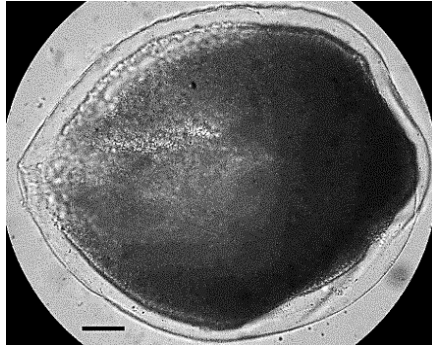


Figure 5.67. *Bathyallogromia* sp. 2 (Scale bar: 50 μm)

Differential diagnosis. The apertural structure of *Bathyallogromia* sp. 2 does not project beyond the general outline of the test. There is no low mound-like structure as in *Bathyallogromia* sp. 1 and other species of the genus. This, and the gap between the test wall and the cell body, cast some doubt on the assignment to *Bathyallogromia*.

Distribution. The species is found in the north-western part of the Black Sea in the depth range of 120-240 m in thin silt with *Phaseolina*. At a depth of 240 m *Bathyallogromia* sp. 2 inhabits in close proximity to methane seeps.

***Allogromiid* sp. 1** (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.68)

Description. The test is elongate, symmetrical, flask-like, with an average length of 240 μm , average width of 95 μm , and coefficient *C* of 2.5. (Fig. 5.68). There is a single aperture at the end of a regular tubular extension with an average length of 25 μm and width of 23 μm . The test wall is slightly agglutinated and semi-transparent.

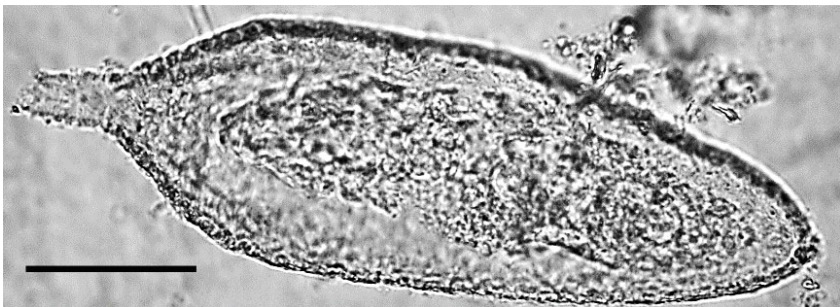


Figure 5.68. *Allogromiid* sp. 1 (Scale bar: 50 μm)

Differential diagnosis. This species differs from other allogromiids in the shape of the test and the thickness of its wall.

Distribution. It is found in the north-western part of the Black Sea at a depth of 150-160 m in silt with an admixture of bivalve shells, as well as in quartz sand.

Allogromiid sp. 3 (Sergeeva, Anikeeva & Gooday, 2010)
(Fig. 5.69)

Description. The test is basically oval with well-developed tubular apertural extensions at both ends (Fig. 5.69). It is 180 μm long, including the tubular extensions, and 70 μm wide, with a coefficient C of about 2.5. The apertural extensions measure 30 x 20 μm and 40 x 20 μm . The wall appears to be organic but is obscured by a dense layer of amorphous detritus.

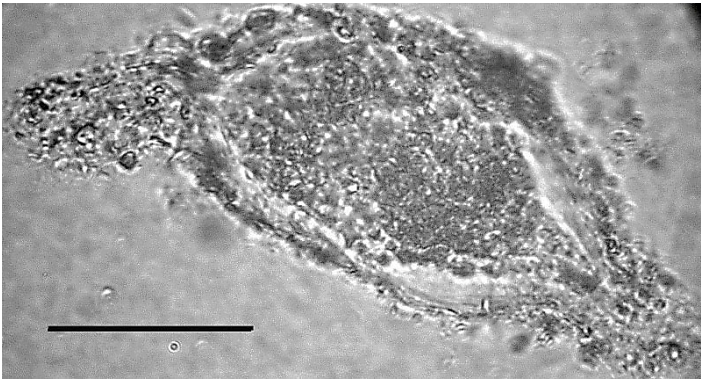


Figure 5.69. Allogromiid sp. 3 (Scale bar: 50 μm)

Differential diagnosis. This morphotype differs from species of *Tinogullmia* genus in the presence of agglutinating material covering the test wall and the greater width of the apertural necks.

Distribution. It is found in the north-western part of the Black Sea at 160 m in silty sand with an admixture of broken mollusc shells.

Allogromiid sp. 4 (Sergeeva, Anikeeva & Gooday, 2010)
(Fig. 5.70)

Description. The test is fairly elongate, 260 to 310 μm long and 90 to 100 μm wide, with a coefficient C of 2.9 and narrowing towards the apertural end (Fig. 5.70). The apertural extension is 25 - 28 μm wide and 25 - 32 μm long. The wall is transparent, thin, without agglutination. The cytoplasm is granular and contains vacuole-like inclusions.

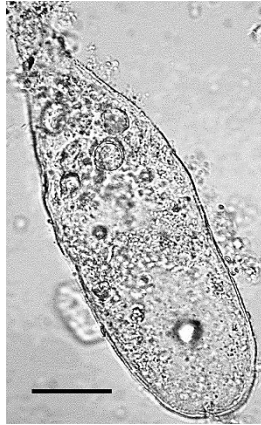


Figure 5.70. Allogromiid sp. 4 (Scale bar: 50 μm)

Differential diagnosis. This species is similar to Allogromiid sp. K except for the absence of a little spur at the end of the aperture. Another difference is the presence of spherical vacuole-like bodies in the cytoplasm of Allogromiid sp. 4 but not of Allogromiid sp. K.

Distribution. It is found in the north-western part of the Black Sea at a depth of 160-180 m in silty sand with an admixture of broken mollusc shells, as well as in plant detritus.

Allogromiid sp. 5 (Sergeeva, Anikeeva & Gooday, 2010)
(Fig. 5.71)

Description. This small allogromiid has an asymmetrically rounded test, measuring 115 μm long and 95 μm wide, with a coefficient C of 1.2 (Fig. 5.71). There is a single small, slightly protruding apertural structure, 14 μm wide and 5-7 μm long. The test wall is transparent. The cytoplasm is homogeneous and granular and separated from the wall by a distinct space.

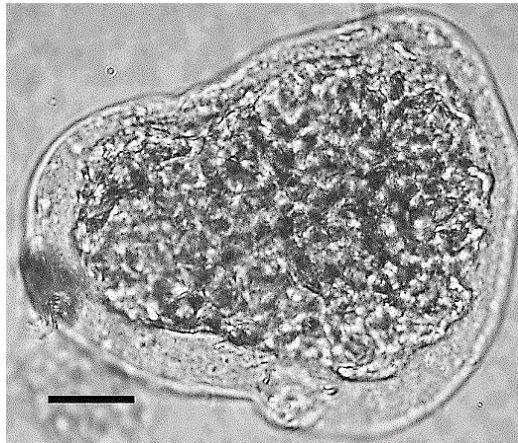


Figure 5.71. Allogromiid sp. 5 (Scale bar: 20 μm)

Differential diagnosis. This morphotype can not be referred to any allogromiid genus.

Distribution. It is found in the north-western part of the Black Sea at a depth of 160 m in silty sand with an admixture of broken molluscs shells.

Allogromiid sp. 6.

(Fig. 5.72)

Description. The test is oval, elongate, measuring 170 - 350 μm long with a coefficient *C* of about 2.5. It narrows somewhat towards the apertural end where a narrow deep channel of the test appears to be associated with the aperture. The wall is organic and transparent. The cytoplasm is heterogeneous, contains undefined dark particles, and does not completely fill the test interior (Fig. 5.72).

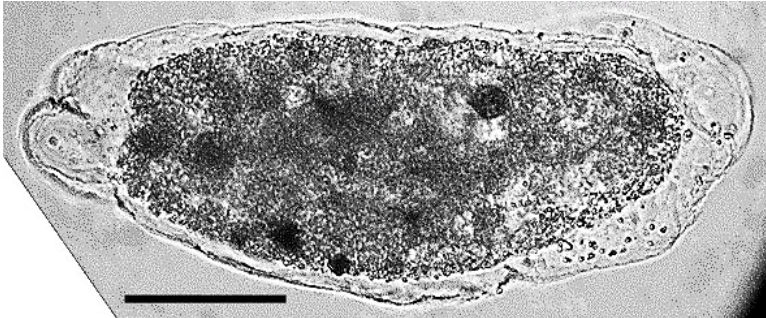


Figure 5.72. Allogromiid sp. 6 (Scale bar: 50 μm)

Differential diagnosis. Allogromiid sp. 6 has some similarity with Allogromiid sp. 40 in terms of the aperture structure, but the test shape is different.

Distribution. It is found in the Black Sea near Sevastopol area at a depth of 11 - 18 m in silty sediments.

Allogromiid sp. 7

(Fig. 5.73)

Description. The test is elongate, 250 - 500 μm long with a coefficient *C* of about 8. It is approximately the same width throughout, although slightly narrowing towards the distal end (Fig. 5.73). The apertural structure is a somewhat bulbous tube with a central thread of cytoplasm. The wall is organic and transparent. The cytoplasm is homogeneous and entirely fills the test cavity. The nucleus is small, located in the centre of the cell.

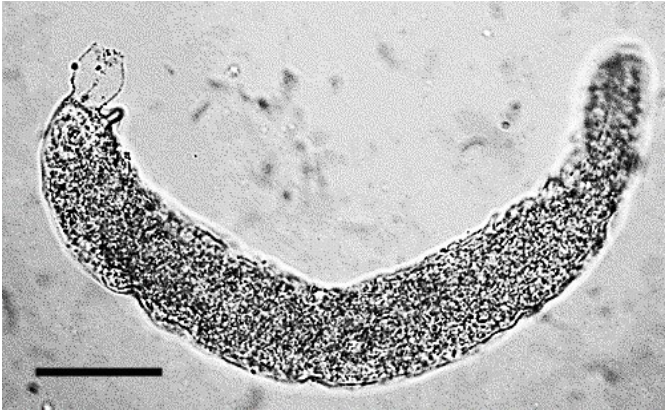


Figure 5.73. Allogromiid sp. 7 (Scale bar: 50 μ m)

Differential diagnosis. In terms of the test shape, this species has some resemblance to *Bowseria arctowskii* Sinniger et al. 2008 from western Antarctica. However, the test size significantly exceeds that of Allogromiid sp. 7 and the apertural structure is quite different.

Distribution. It is found in the Black Sea near Sevastopol area at a depth of 11 - 168 m in silty sediments.

Allogromiid sp. 9 (Sergeeva, Anikeeva & Gooday, 2010)
(Fig. 5.74)

Description. The test is elongate, 515 μ m long and 150 μ m wide, with a coefficient *C* of about 3.4 (Fig. 5.74A). It is wider at the apertural end where the *Vellaria*-like apertural structure (22 μ m long and 33 μ m wide) is located (Fig. 5.74B). The wall is organic, dense, transparent, with indistinct longitudinal striations.

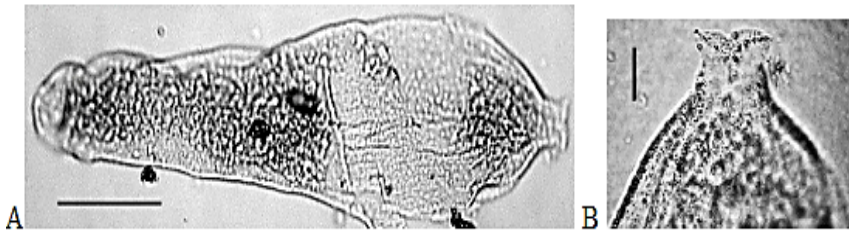


Figure 5.74. Allogromiid sp. 9. A – general view, B – aperture (Scale bar: A – 50 μ m, B – 20 μ m)

Differential diagnosis. The apertural structure is rather similar to that of *Vellaria*. However, the test wall of Allogromiid sp. 9 has longitudinal striations that are not present in *Vellaria*. The size of the test also exceeds that of *Vellaria* species.

Distribution. It is found in the north-western part of the Black Sea at a depth of 160 m in quartz sand with an admixture of broken mollusc shells.

Allogromiid sp. 10 (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.75)

Description. The test is elongate, 340 - 525 μm long and 70 - 115 μm wide (Fig. 5.75A), with a coefficient *C* of 4.5 - 5.6. The single aperture is located at the end of a prominent apertural structure (Fig. 5.75B) that measures 33 μm long and 25 μm wide. The organic test wall is overlain by a thin agglutination veneer. The cytoplasm is homogeneous, completely fills the interior of the test.

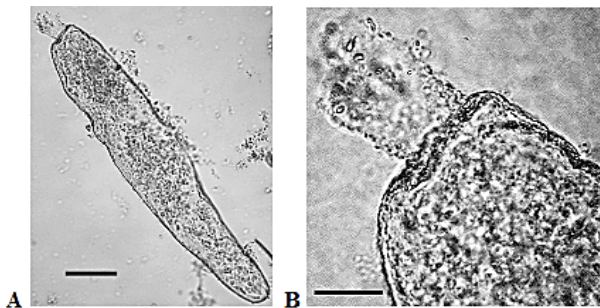


Figure 5.75. Allogromiid sp. 10. A – general view, B – aperture (Scale bar: A – 50 μm , B – 20 μm)

Differential diagnosis. Allogromiid sp. 10 resembles *Vellaria* sp. C in the length of the test and the location of the aperture, but there are differences, mainly in the shape of the test, which is more uniform in width, and the apertural structure.

Distribution. This morphotype was found in the north-western part of the Black Sea at a depth of 150-160 m in quartz sand with an admixture of silt and fragments of mollusc shells, as well as in sandy silt. They were recorded also in the Gulf of Feodosiya at a depth of 26 m, in dense silt with H_2S , detritus and fine sand.

Allogromiid sp. 11 (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.76)

Description. The test is broadly oval (Fig. 5.76A), 320 μm long and 250 μm wide, with a coefficient *C* of about 1.3. The single apertural structure is asymmetrical (Fig. 5.76B), 47 μm long on one side, 12 μm long on the other side and 50 μm wide. The wall is organic and transparent. The cytoplasm is finely granular and separated from the test wall by a large space. The nucleus is 40 μm in diameter and situated at the centre of the cell (Fig. 5.76C).

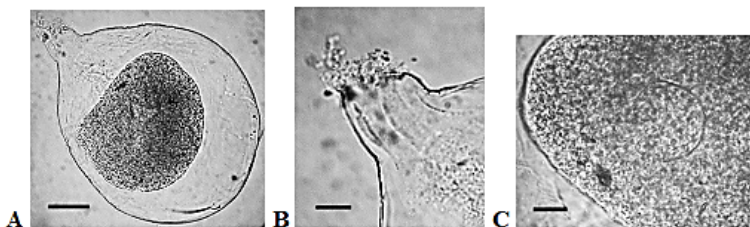


Figure 5.76. Allogromiid sp. 11. A – general view, B – aperture, C – cytoplasm (Scale bar: A – 50 μm , B, C – 20 μm)

Differential diagnosis. Allogromiid sp. 11 resembles *Bathyallogromia* in the shape of the test and the appearance of the wall, but the apertural structure is quite different.

Distribution. It is found in the northwestern part of the Black Sea at a depth of 130 m in *Phaseoline* silt.

Allogromiid sp. 15

(Fig. 5.77)

Description. Allogromiid with an elegant, elongate-oval shape (Fig. 5.77A), length 230 μm , width 110 μm , coefficient *C* about 2. Two apertures are located at opposite ends of the test. One is situated at the end of a curved, tubular structure, length 33 μm (Fig. 5.77B), and the other is a simple round hole with a diameter of 12 μm (Fig. 5.77A). The organic wall is thin and smooth, without agglutinated material. The cytoplasm is pale, homogeneous with a nucleus 23 μm in diameter (Fig. 5.77C).



Figure 5.77. Allogromiid sp. 15. A – general view, B – the aperture of curved formation, C – nucleus (Scale bar: A – 50 μm , B, C – 20 μm)

Differential diagnosis. This morphotype is similar to the genus *Tinogullmia* in terms of the test shape, number and location of apertures. The difference between them is that tinogullmiids have two identical apertures at the ends of tubular structures, while in Allogromiid sp. 15 the apertures are quite different.

Distribution. It is found in the northwestern part of the Black Sea at a depth of 120 m in thin *Phaseolina* silt.

Allogromiid sp. 30 (Anikeeva & Gooday, 2016)

(Fig. 5.78)

Description. The test is elongate, of medium size, measuring 280 x 87 μm , with a coefficient *C* of about 3-3.2 (Fig. 5.78). There appear to be two apertures, ~15 μm in diameter, at opposite ends of the test, but the apertural structures are not obvious. The wall is organic and transparent. The cytoplasm fills much of the test interior and is very heterogeneous. The nucleus, (diameter is about 40 μm), is located in the middle part of the cell.

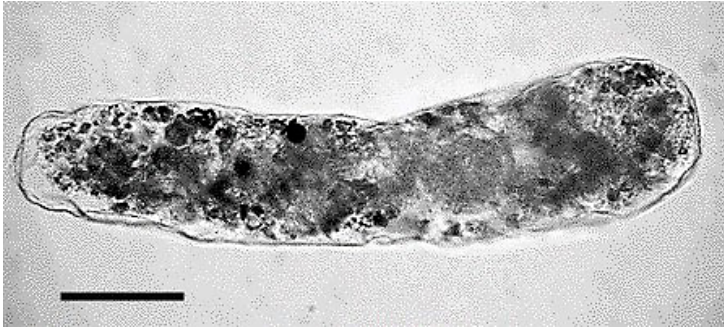


Figure 5.78. Allogromiid sp. 30 (Scale bar: 50 μm)

Differential diagnosis. This morphotype resembles Allogromiid sp. S, but has two rather than one aperture.

Distribution. It is found in the area of Zernov's *Phyllophora* field (NW of the Black Sea; depth 24 - 38 m), as well as in the area of Yalta, Karkinitzky Gulf and Cape Opuk (depth 26 - 95 m) in silt with dead *Phaseolina* shells and black silt with a strong smell of hydrogen sulfide.

Allogromiid sp. 33 (Anikeeva & Gooday, 2016)

(Fig. 5.79)

Description. The test is asymmetrically oval, of medium sized, measuring 300 x 220 μm , with a coefficient C of 1.3. The single aperture is rather inconspicuous, about 16 μm in diameter, and connected to the cell body by a channel. The wall is organic and transparent (Fig. 5.79). The cytoplasm is filled with stercomata and various other inclusions, possibly of a mineral nature. A nucleus was not visible.

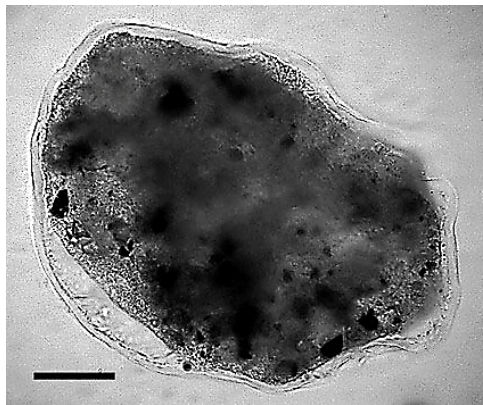


Figure 5.79. Allogromiid sp. 33 (Scale bar: 50 μm)

Differential diagnosis. This morphotype resembles Allogromiid sp. 38 but differs in terms of the apertural structure and presence of cytoplasmic inclusions, as well as being much larger.

Distribution. The species is found in the area of the Zernov's *Phyllophora* field (24-38 m depth) in sandy silt with molluscs shell fragments, as well as in the Karkinitzky Gulf (19 m depth) in similar sediment.

Allogromiid sp. 34 (Anikeeva et al., 2019)
(Fig. 5.80)

Description. The test is elongate oval, length 280 μm , width 98 μm , with a coefficient *C* of about 2.8. (Fig. 5.80). The single aperture (14 μm diameter) is situated at the end of the test where it forms a slight projection with an irregular outer margin. The wall is organic, thin and transparent. The cell body contains dark mineral grains, most of them located near the apertural end.

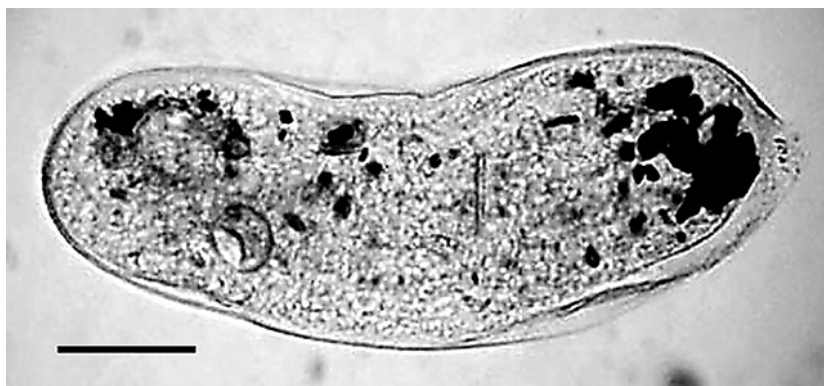


Figure 5.80. Allogromiid sp. 34 (Scale bar: 50 μm)

Differential diagnosis. In terms of the test shape and the appearance of the apertural structure, Allogromiid sp. 34 is rather similar to unnamed organic-walled monothalamids from the bathyal NE Atlantic (Gooday, 1986b; Fig. 1G-I) and the Barents Sea (Gooday et al., 2013; Fig. 4c). It also resembles Allogromiid sp. 30 of Anikeeva & Gooday (2016, Fig. 2A). However, all three of these species lack dark intra-cellular mineral particles. Allogromiid sp. 34 may be related to the genus *Psammophaga*, in which such grains are present. It is distinguished by the fairly elongate, more or less oval test, rather than the droplet-like test that is typical of most *Psammophaga* species.

Distribution. The species is found in the Black Sea in the Yalta region, the Karkinitzky Gulf and the near-Kerch area, at depths between 18 and 87 m in silty sediment with dead *Phaseolina* shells.

Allogromiid sp. 36 (Anikeeva et al., 2019)
(Fig. 5.81)

Description. The test is broadly oval, 360 μm long, 220 μm wide with a coefficient *C* of about 1.6. A nipple-like apertural projection (diameter 26 μm) is situated at one end of the test. The wall is organic, thin and transparent (Fig. 5.81). The cell body contains a large circular inclusion, probably an ingested particle, in addition to smaller dark particles.

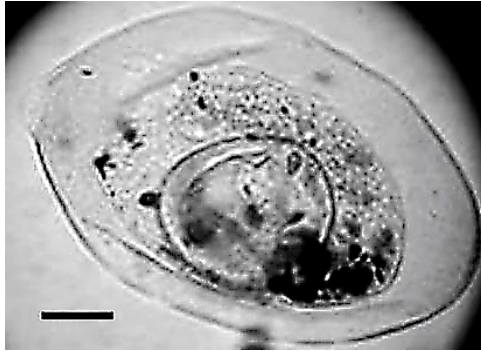


Figure 5.81. Allogromiid sp. 36 (Scale bar: 50 μm)

Differential diagnosis. The oval test shape is reminiscent of Allogromiid sp. N of Sergeeva et al. (2010) from the Dnieper Canyon area (NW Black Sea). However, the form of the aperture and the presence of cytoplasmic inclusions serve to differentiate it.

Distribution. This species is found in the Yalta region of the Black Sea at a depth of 87 m in silty sediment with dead *Phaseolina* shells.

Allogromiid sp. 38

(Fig. 5.82)

Description. The test is irregularly oval in shape, measuring 175 x 107 μm , with a coefficient C of 1.6. (Fig. 5.82A). The single wide aperture (about 26 μm in diameter) is located slightly asymmetrically (Fig. 5.82B) at the end of a convex apertural structure. The wall is organic, thin and transparent. The cytoplasm is light in color, homogeneous, with a small nucleus, about 9 μm in diameter, located closer to the apertural end.

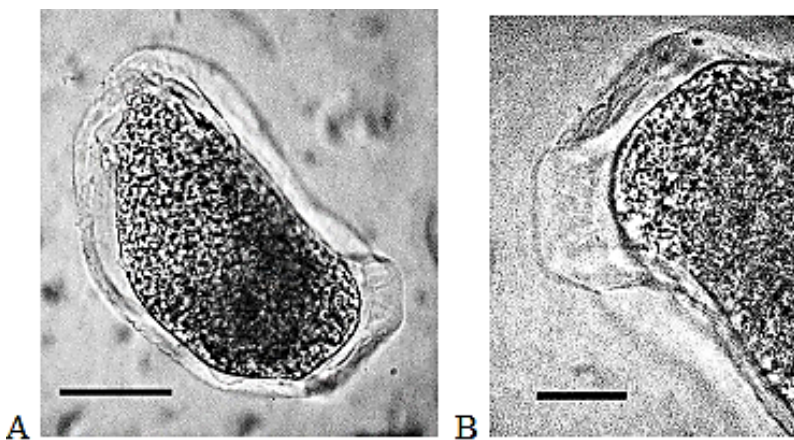


Figure 5.82. Allogromiid sp. 38. A – general view, B – apertural part (Scale bar: A – 50 μm , B – 20 μm)

Differential diagnosis. This morphotype is similar to *Allogromiid* sp. 33, but is considerably smaller (almost half the size) and differs in terms of the apertural structure and the content of the cytoplasm.

Distribution. It is found in the Black Sea near the Zernov's *Phyllophora* field at a depth of 24 m in silted sand with an admixture of molluscs shells.

Allogromiid sp. 39

(Fig. 5.83)

Description. The test is elongate, measuring $286 \times 39 \mu\text{m}$, with a coefficient *C* of about 7.3 (Fig. 5.83A). Two apertures are located at opposite ends of the test; one is at the end of a cylindrical neck (as in *Vellaria*) measuring $26 \times 10 \mu\text{m}$ (Fig. 5.83B), the other is a simple hole, about $18 \mu\text{m}$ in diameter, located in a depression (Fig. 5.83C). The test wall is organic, thin and transparent. The cytoplasm is pale, finely granular and homogeneous.

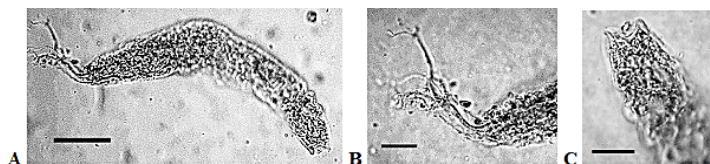


Figure 5.83. *Allogromiid* sp. 39. A – general view, B, C – the apertures (Scale bar: A – $50 \mu\text{m}$, B, C – $20 \mu\text{m}$)

Differential diagnosis. *Allogromiid* sp. 39 is similar to *Vellaria* sp. C, but has two apertures rather than only one.

Distribution. It is found in the Black Sea in the Feodosiya Gulf at a depth of 26 m in dense silt with a smell of H_2S , as well as in detritus and fine sand.

Allogromiid sp. 40

(Fig. 5.84)

Description. The test is small, oval and measures $120 \times 75 \mu\text{m}$ with a coefficient *C* of about 1.6. The aperture is located at one end on a short, wide neck, measuring $29 \times 16 \mu\text{m}$ (Fig. 5.84). The wall is organic, thick and transparent. The cytoplasm is finely granulated, pale, and homogeneous, with a large distinct nucleus (diameter $23 \mu\text{m}$) situated closer to the aperture.

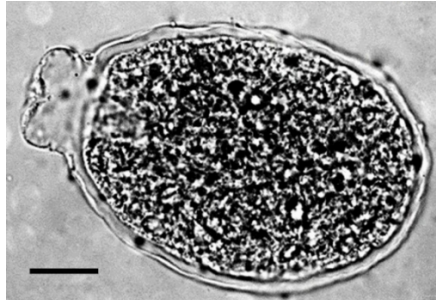


Figure 5.84. Allogromiid sp. 40 (Scale bar: 20 μm)

Differential diagnosis. Allogromiid sp. 40 is similar to Allogromiid sp. M in terms of the test shape, but differs in features such as the cytoplasmic contents, apertural structure and the test wall, which is purely organic.

Distribution. It is found in the Sivash Gulf (the Sea of Azov) at a depth of 0.6 m on a silty sediment with molluscs shell fragments and plant detritus. The salinity is 40‰.

Allogromiid sp. 42

(Fig. 5.85)

Description. The test is relatively small, measuring 265 x 145 μm , with a droplet-like shape and a coefficient C of about 1.8 (Fig. 5.85A). The single aperture is located at the narrower end of the test and is associated with a bulbous projecting structure, measuring 27 x 38 μm and resembling a blossoming tulip (Fig. 5.85B). The wall is organic and transparent. The cytoplasm is very finely granular, pale, homogeneous and contains small amounts of transparent inclusions, possibly quartz particles.

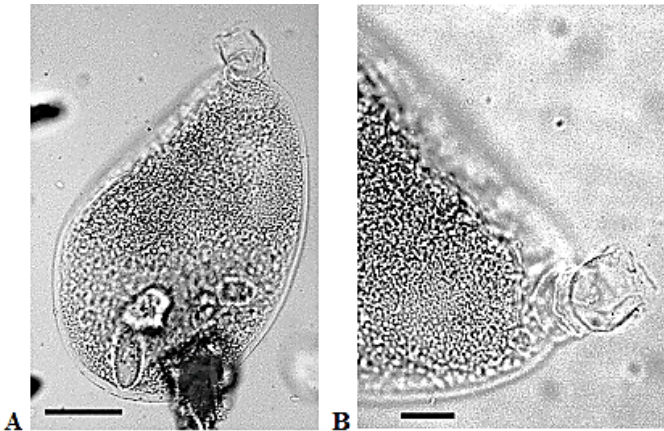


Figure 5.85. Allogromiid sp. 42. A – general view, B – apertural part (Scale bar: A – 50 μm , B – 20 μm)

Differential diagnosis. This morphotype is rather like Allogromiid sp. 7 in terms of the apertural structure but the test shapes are completely different.

Distribution. It is found in the Sivash Gulf (the Sea of Azov) at a depth of 1 m and salinity of 10‰ on silt with mollusc shell fragments and detritus. Also in the Sea of Azov at a depth of 8 m in the silty sediment.

Allogromiid sp. A

(Fig. 5.86)

Description. The test is elongate, measuring 242 x 52 µm with a coefficient *C* of 4.6. The inflated apertural end is much wider than the rest of the test (Fig. 5.86A). The single aperture is on a short neck, measuring 10 x 8 µm, located at the wider end of the test (Fig. 5.86B). The wall is organic, transparent and thin. The cytoplasm is homogeneous and finely granulated. The nucleus is small (diameter is 10 µm) and located in the middle part of the test.

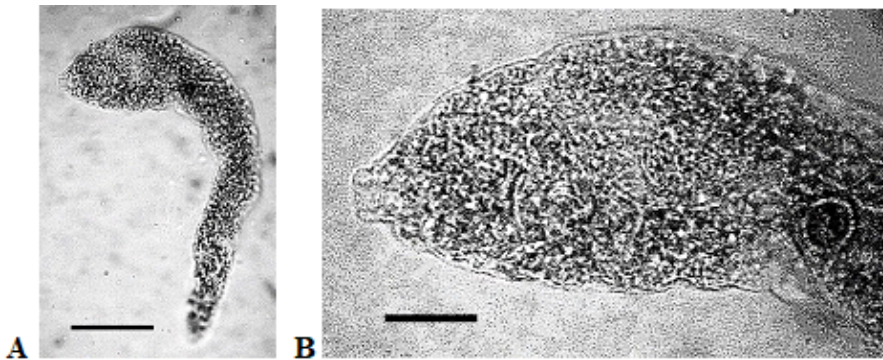


Figure 5.86. Allogromiid sp. A. A – general view, B – apertural part and nucleus (Scale bar: A – 50 µm, B – 20 µm)

Differential diagnosis. This morphotype resembles *Vellaria* sp. C and Allogromiidae gen. sp. 10, but is distinguished by the expanded anterior part of the test as well as differences in the aperture necks.

Distribution. The morphotype is found in the Black Sea near Cape Opuk at a depth of 96 m in dense silt with detritus and a broken mollusc shells.

Allogromiid sp. E [Syn. Allogromiidae gen. sp. E (Sergeeva & Anikeeva, 2006)]

(Fig. 5.87)

Description. Small, almost spherical test with an average length of 160 µm, width 130 µm and coefficient *C* of about 1.2 (Fig. 5.87A, B). There are two barely visible apertures associated with two enlarged inner tubules that open outwards at the ends of the cell body. The wall is organic and transparent. The cytoplasm is homogeneous, finely granular, and some specimens contain mineral particles. The diameter of the nucleus is approximately 32 µm.

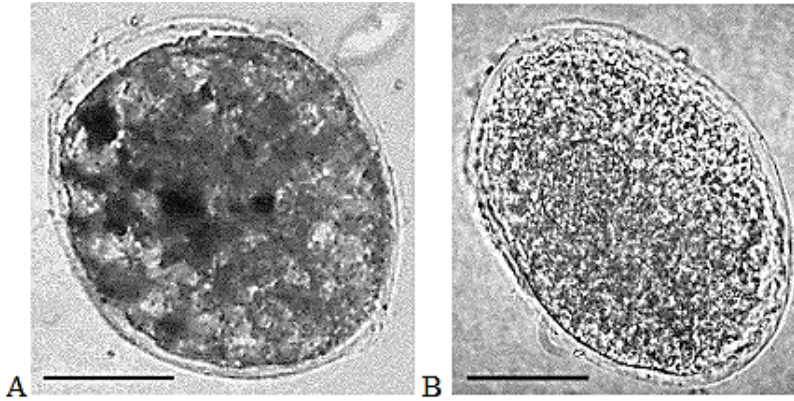


Figure 5.87. Allogromiid sp. E. A, B – general view of two different specimens (Scale bar: 50 μm)

Differential diagnosis. Similar foraminifera are mentioned in the article (Goody et al., 2001) as psammospherids, the distinctive features of which are a spherical test shape and a lack of obvious apertures. Most specimens of Allogromiid sp. E have tests that are somewhat oblong, rather than spherical.

Distribution. Morphotype is found in the Black Sea both in shallow water (at depths from 4 to 14 m) and in deep water (150-170 m) in silt with plant detritus and fine sand with admixture of mollusc shells.

Allogromiid sp. F (Sergeeva & Anikeeva, 2014; Anikeeva et al., 2019) (Fig. 5.88)

Description. The test is small, measuring 210 x 110 μm , and symmetrical oval in shape, with a coefficient C of 1.9 (Fig. 5.88). The aperture is 25 μm in diameter and is located on a 40 μm long neck. The wall is organic, smooth, without agglutination. The cytoplasm is homogeneous, fine-grained and contains small inclusions, some of which are similar to quartz particles. The diameter of the nucleus is 33 μm .

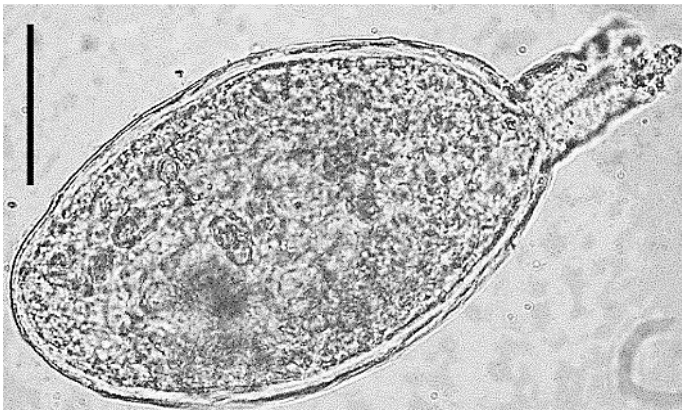


Figure 5.88. Allogromiid sp. F (Scale bar: 50 μm)

Differential diagnosis. This morphotype is similar to the genus *Allogromia* in terms of the test shape, but there are significant differences in the apertural structure.

Distribution. It is found in the Black Sea at a depth of 4 m in sandy sediments (Sevastopol region) and in the Karkinitsky Gulf at a depth of 19 m in silty sediments with molluscs shell fragments.

Allogromiid sp. G (Anikeeva & Gooday, 2016; Anikeeva et al., 2019)
(Fig. 5.89)

Description. The test ranges from oval to spindle-shaped and measures 220-330 μm long and 110-140 μm wide on average with a coefficient *C* of about 2.2. (Fig. 5.89). There are two small, relatively simple terminal apertures, one more prominent than the other, and 3 - 10 μm in diameter. The test wall is transparent, organic, and devoid of agglutinated particles. The cytoplasm contains numerous inclusions, including dark mineral grains that are distributed throughout the cell.

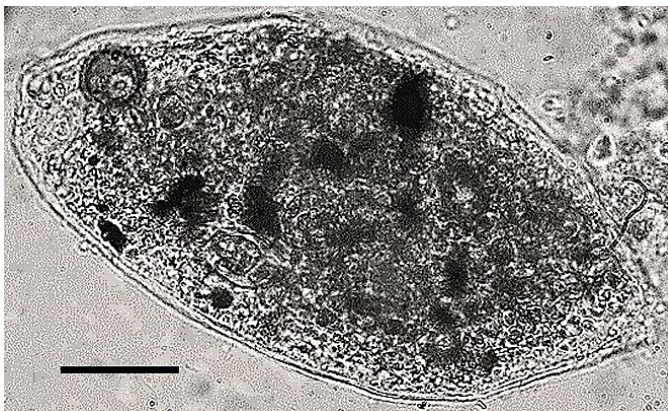


Figure 5.89. Allogromiid sp. G (Scale bar: 50 μm)

Differential diagnosis. Morphologically, Allogromiid sp. G don't correspond to any genus of the subfamily Shephardellinae.

Distribution. The morphotype was first observed in the Black Sea near Sevastopol (Uchkuevka) at a depth of 13-25 m. Later it was found in Bosphorus region, in the area of the Zernov's *Phyllophora* Field, in the area of Yalta, Feodosia, Cape Opuk and in the Karkinitsky Gulf in the depths range of 22-95 m. It inhabits sediment with detritus or large pebbles, sand, silty sand with plant detritus, silt with detritus, silt with mollusc shell fragments.

Allogromiid sp. J (Sergeeva, Anikeeva & Gooday, 2010)
(Fig. 5.90)

Description. The test is elongate, 265 μm long, 100 μm wide with a coefficient *C* of about 2.6. The broadly-rounded proximal end tapers towards the single aperture at the bluntly pointed distal end (Fig. 5.90). The aperture is simple and $\sim 18\mu\text{m}$ wide. The cytoplasm incorporates some vacuole-like inclusions and a few dark particles.

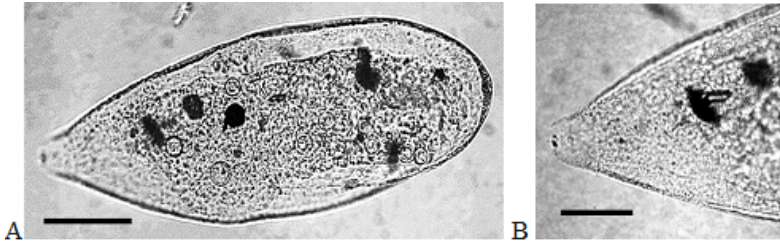


Figure 5.90. Allogromiid sp. J. A – general view, B – apertural part (Scale bar: 50 μm)

Differential diagnosis. Allogromiid sp. J resembles Allogromiid sp. 1 in terms of the shape of the test, but is distinguished by the aperture structure and the much thinner test wall.

Distribution. The morphotype is found in the northwestern part of the Black Sea at a depth of 120 m in thin *Phaseolina* silt.

Allogromiid sp. K (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.91)

Description. The test varies from oval to slightly elongate and tapers towards the apertural end (Fig. 5.91A). It is 290 – 350 μm long and 60 – 120 μm wide, with a coefficient *C* of about 2.9-4.8. The apertural structure is prominent, cylindrical before tapering to a terminal spur (Fig. 5.91B). It measures about 50 μm long and 30 μm wide. The test wall is transparent, although some specimens have a thin agglutinated layer.

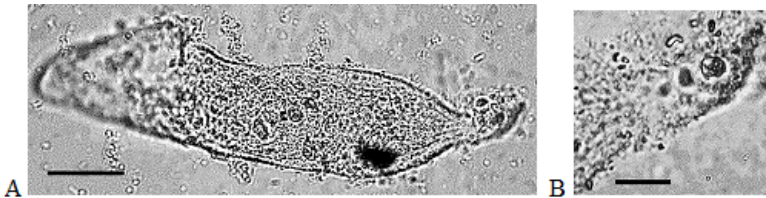


Figure 5.91. Allogromiid sp. K: A – general view, B – apertural part (Scale bar: A – 50 μm , B – 20 μm)

Differential diagnosis. This morphotype is compared above with Allogromiid sp. 4.

Distribution. This morphotype is found in the Black Sea both in shallow water (5-8 m) in closed bays and in hypoxic waters at a depth of 160 m in the open sea. It is found on sandy silts and in coarse silica sand with an admixture of mollusc shells.

Allogromiid sp. L (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.92)

Description. The test measures 240 μm long and 80 μm wide with a coefficient *C* of 3. It has a distinctive elongate and approximately oval shape, tapering slightly from the proximal to the distal end (Fig. 5.92 A). The proximal end is drawn out into a short, pointed tail-like feature. The single aperture is located at the end of a

prominent apertural extension (35 x 23 μm), rather similar in shape to that of *Vellaria* (Fig. 5.92B). The cytoplasm is coarse-grained, and homogenous.

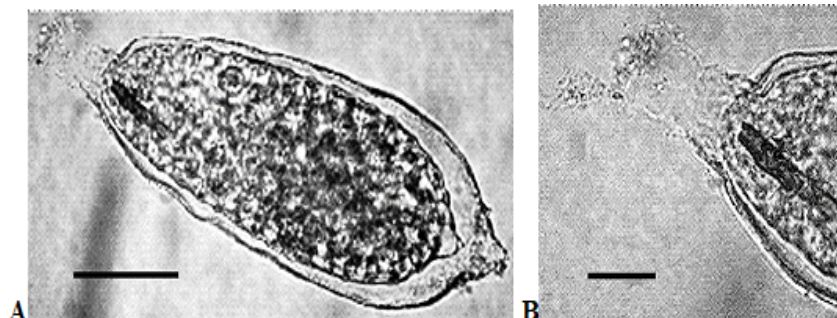


Figure 5.92. Allogromiid sp. L. A – general view, B – apertural part (Scale bar: A – 50 μm , B – 20 μm)

Differential diagnosis. Despite the similarity of the aperture structure, this morphotype differs from *Vellaria* in the nature of its cytoplasm and the shape of the test.

Distribution. It occurs in the Black Sea both in shallow water (5-19 m) and at a depth of 240 m in detritus, sandy silt, black pelite silt with hydrogen sulphide. It is found in areas associated with methane seeps.

Allogromiid sp. M

(Fig. 5.93)

Description. The test is oval, measuring 290 x 160 μm , with a coefficient *C* of 1.8. The single, wide apertural structure has a diameter of 35 μm (Fig. 5.93B) and projects beyond the test contour. The peduncular sheath extends some 70 μm into the cell body. The wall is organic with some adhering particles around the aperture (Fig. 5.93A). The cytoplasm is homogeneous, dark in color.

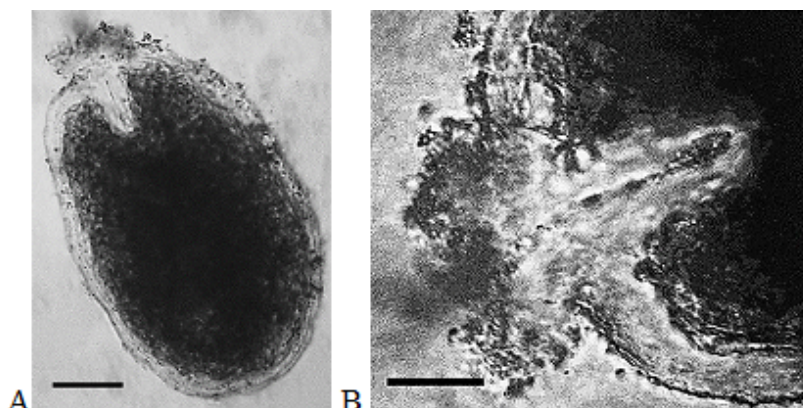


Figure 5.93. Allogromiid sp. M: A – general view, B – apertural part (Scale bar: A – 50 μm , B – 20 μm)

Differential diagnosis. This morphotype can not be referred to any known allogromiid genus.

Distribution. It is found in the Black Sea in shallow water (3-5 m) near the Kruglaya Bay (Sevastopol) in coarse silty sand with mollusc shell fragments.

Allogromiid sp. N (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.94)

Description. The test is approximately oval and slightly asymmetrical, measuring 265 μm long and 120 μm wide (Fig. 5.94) with a coefficient C of about 2.2. The proximal end is gently curved and there is a single aperture situated at the distal end. The cytoplasm is homogeneous, it is separated from the test wall by a distinct and fairly wide space.

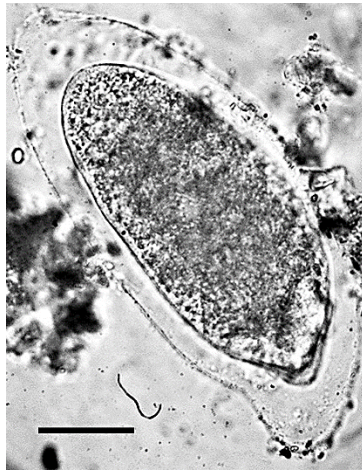


Figure 5.94. Allogromiid sp. N (Scale bar: 50 μm)

Differential diagnosis. This morphotype cannot be assigned to any of the known allogromiid genus.

Distribution. This morphotype is found at shallow depths in Sevastopol bays and in hypoxia waters at a depth of 160 m in the north-western part of the Black Sea. It is found in silty sands and coarse quartz sand with an admixture of mollusc shells, as well as in black hydrogen sulphide silt.

Allogromiid sp. Q

(Fig. 5.95)

Description. The test is somewhat oblong with an approximately uniform width and measuring 260 x 70 μm with a coefficient C of 3.7 (Fig. 5.94A). It has one aperture (diameter 15 μm) located at the end of a characteristically shaped neck that measures 25 μm wide at the expanded base and 23 μm long (Fig. 5.95B). The wall is translucent with some agglutination. The cytoplasm is pale and homogeneous.

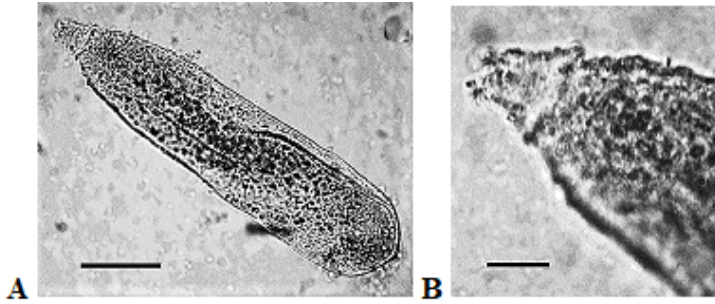


Figure 5.95. Allogromiid sp. Q. A – general view, B – apertural part (Scale bar: A – 50 μm , B – 20 μm)

Differential diagnosis. This morphotype cannot be assigned to any of the known allogromiid genus.

Distribution. It is found in the Black Sea at a depth of 120 m in thin silt with an admixture of *Phaseolina* shells.

Allogromiid sp. R (Anikeeva et al., 2019)

(Fig. 5.96)

Description. The test is long, tubular in shape (Fig. 5.96A), measuring 480 x 50 μm with a coefficient *C* of 9.6. The wall is organic, thin and transparent. Two dissimilar apertures are situated on opposite ends of the test (Fig. 5.96B, C). One is located on the short neck, and the other is a simple hole at the end of the test. Their diameters range from 12 to 14 μm .

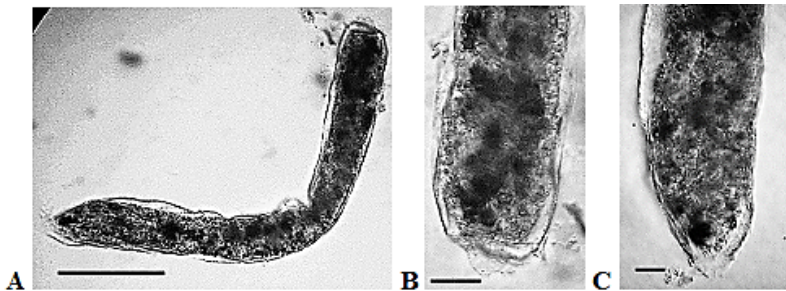


Figure 5.96. Allogromiid sp. R. A – general view, B, C – the apertures (Scale bar: A – 50 μm , B, C – 20 μm)

Differential diagnosis. Allogromiid sp. R has some slight resemblance to the genus *Nemogullmia* but is much shorter and not thread-like in shape. The main feature that distinguishes this morphotype from the genus *Tinogullmia* is the structure of apertures.

Distribution. It is found in the Black Sea near Yalta at a depth of 81-87 m in the silt bottom sediments with *Phaseolina* shells.

Allogromiid sp. S (Anikeeva & Gooday, 2016)

(Fig. 5.97)

Description. The test is elongate and asymmetrical (Fig. 5.97), measuring 160 x 55 μm with a coefficient C of 2.9. The single aperture is associated with a narrow, inconspicuous canal, 3-4 μm in diameter, located at the narrower end of the test. The wall is thin, smooth, protein, without agglutination. The cytoplasm is heterogeneous, with mineral inclusions and stercomata.

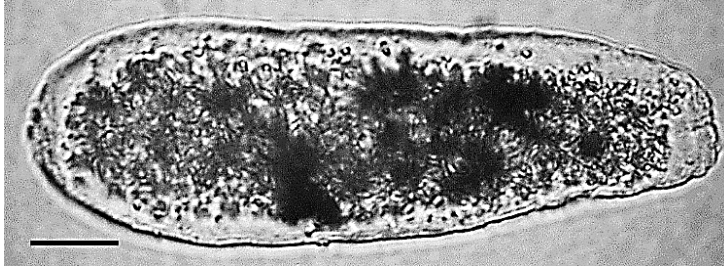


Figure 5.97. Allogromiid sp. S (Scale bar: 20 μm)

Differential diagnosis. This morphotype cannot be assigned to any of the known allogromiid genus.

Distribution. It is found in the Black Sea at a depth of 120 m in *Phaseolina* silt, as well as in the area of Zernov's *Phyllophora* field at a depth of 38 m in silty sand with mollusc shell fragments.

Allogromiid sp. Y (Sergeeva, Anikeeva & Gooday, 2010)

(Fig. 5.98)

Description. The test is broadly oval, 180 μm long and 80 μm wide with a coefficient C of 2.2 (Fig. 5.98). The single aperture is barely discernible and about 10 μm wide. The test wall is thin and devoid of agglutinated material. The cytoplasm is homogeneous, in places with a considerable gap between test wall and the cell body.

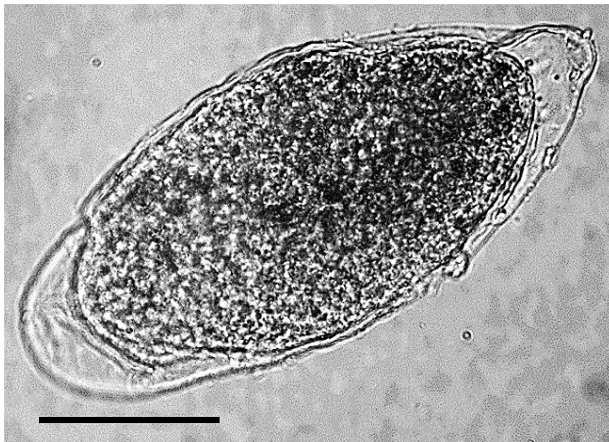


Figure 5.98. Allogromiid sp. Y (Scale bar: 50 μm)

Differential diagnosis. This morphotype cannot be assigned to any of the known allogromiid genus.

Distribution. It is found in the northwestern part of the Black Sea at a depth of 130 m in *Phaseolina* silt.

Allogromiid with 3 apertures (Sergeeva, Anikeeva & Gooday, 2010)
(Fig. 5.99)

Description. The test is elongate and more or less parallel sided (Fig. 5.99); the three specimens are 238-403 μm long and 65 μm wide with a coefficient *C* of 3.6 - 6.2. One end is drawn out into a long apertural tube, $\sim 37\mu\text{m}$ long; two smaller protuberances with small terminal apertures are developed at the other end. The test wall is transparent. The cell body is finely granular with a single nucleus, 21-37 μm diameter, located near the middle.

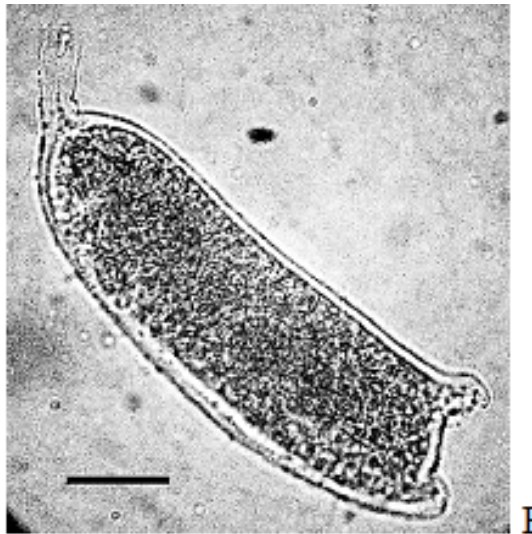


Figure 5.99. Allogromiid with 3 apertures (Scale bar: 50 μm)

Differential diagnosis. This may be an aberrant form of *Tinogullmia* sp., although this possibility is made less likely by the occurrence of specimens at different water depths. This suggests that they are more likely to refer to a new species. This is also indicated by the discovery (Habura et al., 2008) of allogromiids with three apertures on the east coast of the USA (Sapelo Island, Georgia).

Distribution. It is found in the north-western part of the Black Sea at a depth of 120 and 160 m in silt with an admixture of mollusc shells, in quartz sand, as well as fine *Phaseolina* silt with hydrogen sulphide.

CHAPTER 6
TAXONOMIC REVIEW OF THE GROMIIDS IN THE BLACK SEA
AND THE SEA OF AZOV

6.1. General characteristics of the gromiids morphology



Figure 6.1. Main gromiid morphotypes according to the scientific literature. *G. psammophila*, *G. amygdaliformis*, *G. landrethi* (after Gooday et al., 2022), *G. oviformis*, *G. elongata* (photos are taken from WoRMS)

RHIZARIA Cavalier-Smith, 2002.

ENDOMYXA Cavalier-Smith, 2002.

Class GROMIIDEA Cavalier-Smith, 2003.

Order GROMIIDA Claparede & Lachmann, 1856.

Family GROMIIDAE Reuss, 1862.

Gromia Dujardin, 1835.

6.2. Morphological review of gromiids in the Black Sea and the Sea of Azov

Gromia sp. 1
(Fig. 6.2)

Description. The test is almost spherical, measuring 280 x 220 μm , with a coefficient *C* of approximately 1.3 and a single aperture, diameter about 15 μm . The wall is organic, thin, transparent, slightly agglutinated with detritus. The cytoplasm is homogeneous, light brown, the nucleus is not visible.

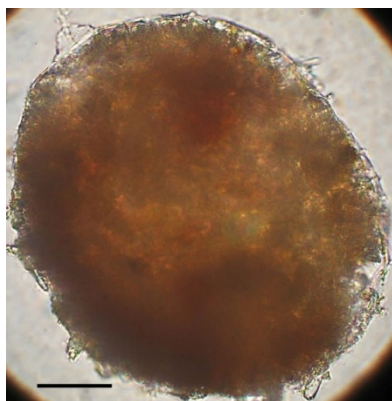


Figure 6.2. *Gromia* sp. 1 (Scale bar: 50 μm)

Differential diagnosis. This morphotype occurs quite often in the Black Sea. Morphologically, *Gromia* sp. 1 is closest to *Gromia landrethi* Gooday et al. 2022 from South Georgia fjords (Fig. 6.1), but the test wall not so smooth. Without molecular analysis, it is difficult to know if there is any relationship between these species.

Distribution. This species was found in an experimental mussel farm in Karantinnaya Bay (near Sevastopol). Collectors, in the form of kapron nets, 5 m high, were located 20 m from the shore and 10 m from the bottom.

Gromia sp. 2
(Fig. 6.3)

Description. The test is egg-shaped (Fig. 6.3A), measuring 535 x 375 μm with a coefficient *C* of about 1.4. There is one nipple-like oral capsule, 60 μm in diameter. The wall is thin with a partial veneer of detritus (Fig. 6.3B). The cytoplasm is well-stained by Rose Bengal and is separated from the wall by a narrow space.

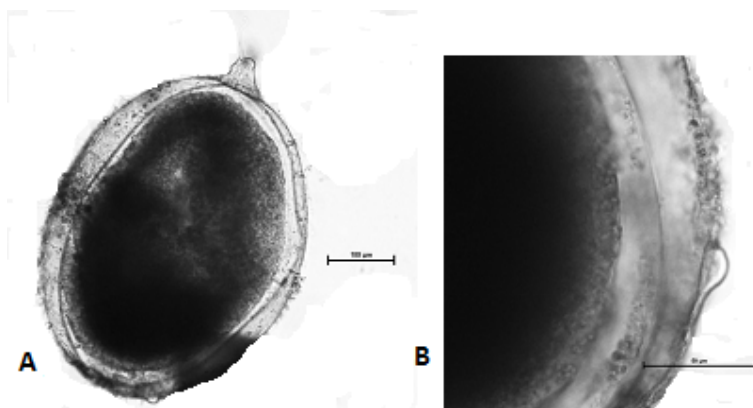


Figure 6.3. *Gromia* sp. 2. A – general view, B – part of the test's wall (Scale bar: A – 100 μm , B – 50 μm)

Differential diagnosis. This species resembles some specimens that have been identified as *Gromia oviformis*.

Distribution. It is found in Sevastopol Bay (St. 15) in black pelitic silty sediments at the depth of 15 m.

Gromia sp. 3

(Fig. 6.4)

Description. More or less spherical gromiid, measuring 940 x 810 μm with a coefficient C of 1.16 (Fig. 6.4A). There is a single protruding oral capsule (Fig. 6.4B), 95 μm in diameter. The test wall is smooth and fragile and slightly broken at the distal end in the illustrated specimen. The cytoplasm is filled with dark stercomata.

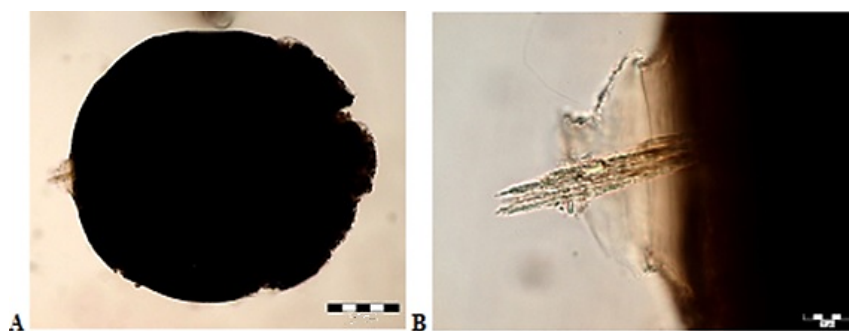


Figure 6.4. *Gromia* sp. 3. A – general view, B – aperture (Scale bar: A – 200 μm , B – 20 μm)

Differential diagnosis. *Gromia* sp. 3 is morphologically similar to *Gromia landrethi* Gooday et al., 2022 in the form of the test, but in the absence of genetic data it is not possible to conclude anything about the relationship between the two species.

Distribution. This species was found in Bosphorus region, at the depth of 82 m in pelitic silt (in the upper one-centimeter layer of bottom sediment).

Gromia sp. 4

(Fig. 6.5)

Description. The test is broadly oval, measuring 450 x 300 μm , with a coefficient *C* of 1.5. This species is characterised by two oral capsules, about 25-30 μm diameter, located at opposite ends of the test. The test wall is thin and organic. The cytoplasm is dense, homogeneous and dark brown.

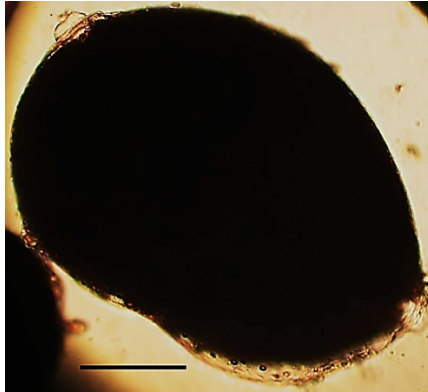


Figure 6.5. *Gromia* sp. 4 (Scale bar: 100 μm)

Differential diagnosis. This morphotype does not resemble any described gromiid species.

Distribution. This species was found in an industrial-experimental mussel farm in Karantinnaya Bay (near Sevastopol). Collectors, in the form of kapron nets, 5 m high, were located 20 m from the shore and 10 m from the bottom.

Gromia sp. 5

(Fig. 6.6)

Description. The test is spherical, about 520 μm in diameter with a coefficient *C* of about 1.1 (Fig. 6.6A). There is a small transparent nipple-like oral capsule with a diameter of about 28 μm (Fig. 6.6B). The wall is thin and smooth and the test is full of stercomata.

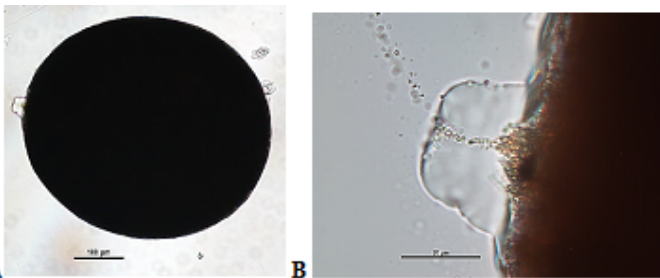


Figure 6.6. *Gromia* sp. 5. A – general view, B – oral capsule (Scale bar: A – 100 μm , B – 20 μm)

Differential diagnosis. *Gromia* sp. 5 resembles two other spherical species, *G. sphaerica* of Gooday et al. (2000) and *G. marmorea* of Rothe et al. (2009), in terms of the test shape, but it lacks the multiple apertures of the former and the mottled appearance of the latter species. It is also smaller than both, particularly *G. sphaerica*, which is one of the largest known gromiids.

Distribution. Anthropogenic underground channel in Balaklava Bay; Istanbul Strait (Bosphorus)s outer area of the Black Sea (Turkish shelf), depth 123 m.

Gromia sp. 6
(Fig. 6.7)

Description. The test is large, 1.03 mm long and 0.5 mm wide (Fig. 6.7A), with a coefficient *C* of about 2. Not less than sixteen oral capsules (Fig. 6.7B, C, D) with a diameter of about 100 μm are distributed along different parts of the test. They are fairly noticeable project above the test surface. The test has a thin and transparent wall, and the interior is filled tightly with dark stercomata.

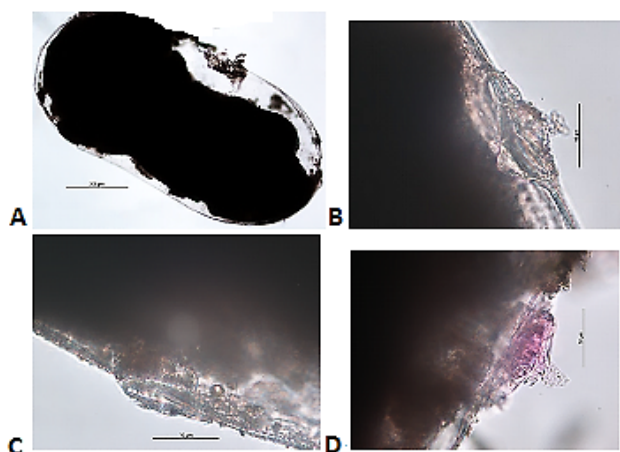


Figure 6.7. *Gromia* sp. 6: A – general view, B, C, D – the oral capsules (Scale bar: A – 200 μm ; B, C, D – 50 μm)

Differential diagnosis. This morphotype does not resemble any known gromiid species.

Distribution. The Black Sea, Cape Aya (Crimea), Ekaterininsky grotto, benthic biofouling (Bivalvia, Bryozoa, Porifera), depth 4 m.

Gromia sp. 7
(Fig. 6.8)

Description. The test is broadly oval, measuring 625 x 500 μm . The oral capsule is flat and wide (170 x 54 μm). The organic wall is thin and transparent; the test contents is homogenous and brownish.



Figure 6.8. *Gromia* sp. 7 (Scale bar: 100 μ m)

Differential diagnosis. This morphotype does not resemble any known gromiid species.

Distribution. The species inhabits the Black Sea in the Gulf of Kalamitsky at a depth of 16 m in the seashell biotope, as well as in the SW and NW areas of the Crimean shelf at the depths of 84-123 m.

Gromia sp. 8
(Fig. 6.9)

Description. The test is small, about 200 μ m in diameter, and spherical with one oral capsule (diameter 50 μ m). The cytoplasm is dark, homogeneous.

Differential diagnosis. This gromiid is similar to *G. sphaerica* in shape, but is much smaller and has only one aperture.

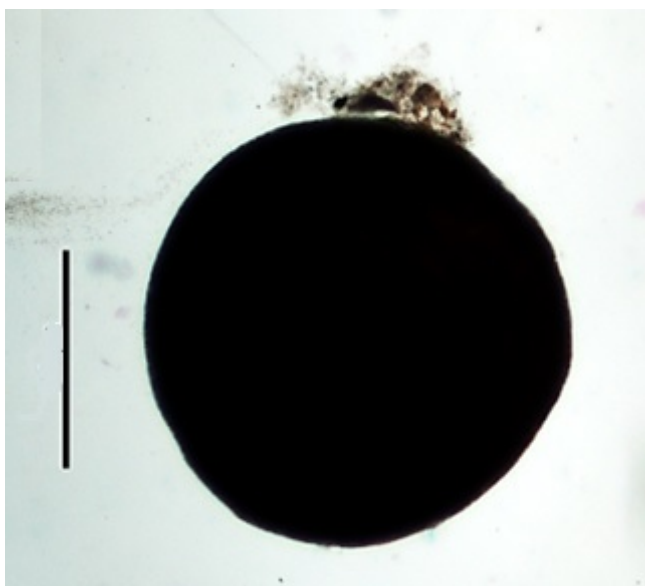


Figure 6.9. *Gromia* sp. 8

Distribution. The species inhabits Cape Aya (the Black Sea, Crimea), underwater Ekaterininsky grotto. It was found in fouling of Bryozoa and Hydrozoa on grotto walls at depths of 1 to 5 m.

Gromia sp. 9
(Fig. 6.10)

Description. The test is fairly elongated 375 x 175 μm in size with a coefficient *C* of about 2. The single oral capsule (diameter 40 μm) is located at the narrower end of the test. The wall is thin, transparent. Homogeneous brownish cytoplasm is evenly distributed within the cell.



Figure 6.10. *Gromia* sp. 9 (Scale bar: 50 μm)

Differential diagnosis. Morphologically, this species does not resemble any of the known *Gromia* species.

Distribution. The species was found in the near Kerch region at a depth of 37 m in silty sediment with mussel shell fragments and detritus.

Gromia sp. 10

(Fig. 6.11)

Description. The test is fragile and relatively large, measuring 1330 x 715 μm , with a coefficient *C* of about 1.8. The oral capsule is 45 μm in diameter. Test wall is encrusted with tiny mineral grains. Inside the cell there are endosymbionts (genus *Symbiodinium* fam. Symbiodiniaceae), these are dinoflagellates (zooxanthellae).

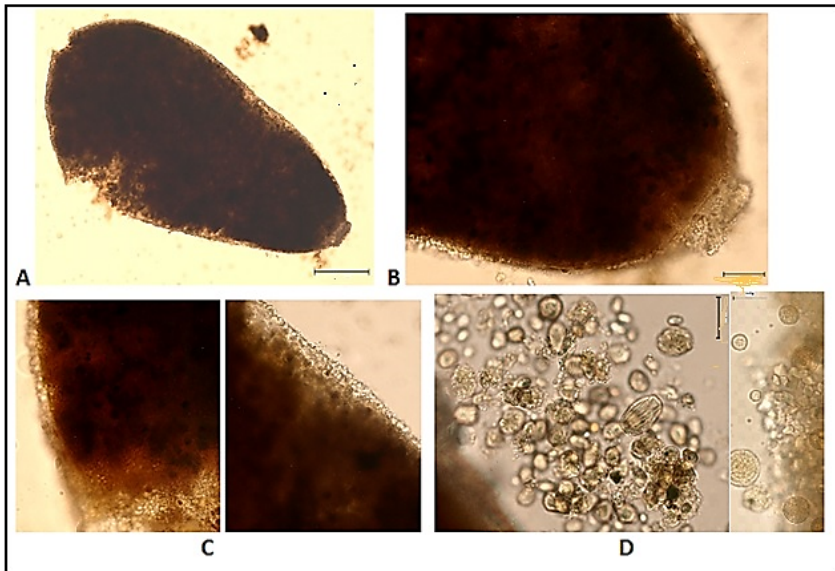


Figure 6.11. *Gromia* sp. 10. A – general view, B – oral capsule, C – internal and external test structure, D – endosymbionts (scale bar: A – 200 μm , B- D – 20 μm)

Differential diagnosis. *Gromia* sp. 10 does not resemble any of the known *Gromia* species on morphological features.

Distribution. It was detected in methane seepage area in SW part of Crimean shelf at the depth 130 m in pelitic silt (Cruise RV “Meteor”, 02.03.2007).

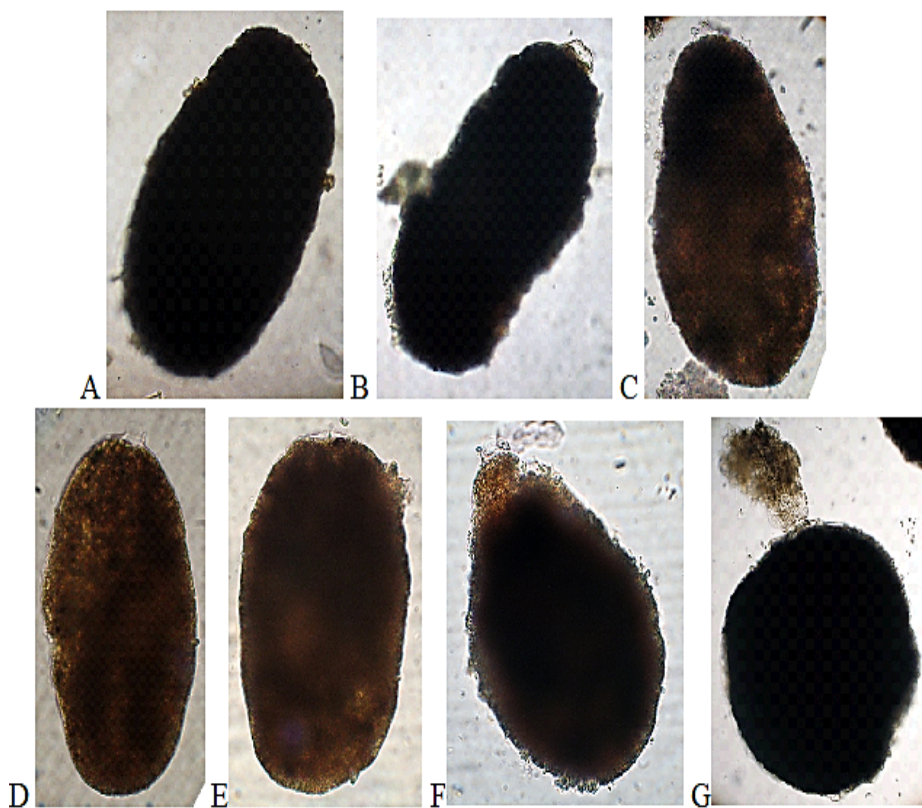


Figure 6.12. Other gromiids from the Black Sea (dimensions are missed): A, B – specimens from the Bosphorus region (cruise RV “Maria S. Merian”, 04.2010, st. 235, depth 160 m, pelitic silt); C-F – specimens from the industrial-experimental mussel farm in Karantinnaya Bay (coastal part of Sevastopol); G–96 cruise of RV “Prof. Vodyanitsky”, Black Sea, st. 42, near-Kerch area, depth 30m.

CHAPTER 7

DISTRIBUTION OF SOFT-WALLED FORAMINIFERA AND GROMIIDS IN THE BLACK SEA ACROSS THE DEPTH GRADIENT FROM NORMOXIA TO CONSTANT HYPOXIA AND ANOXIA

The Black Sea is a body of water adjoining the Mediterranean Sea, but with a sharply defined and anomalous character. Its considerable depth, the great dilution by fresh river waters, and the inflow of deep saline water from the Sea of Marmara, create a sharp salt stratification of the Black Sea water into an upper, relatively thin layer inhabited by rich flora and fauna, and a thick deeper mass (from a depth of 150-250 m to the bottom of the basin) with a high hydrogen sulfide content. The deep hydrogen sulfide waters of the Black Sea are separated from the oxygen zone by an intermediate layer ("suboxic" layer), which extends vertically for meters, if not tens of metres, where both gases coexist in small amounts (Vinogradov and Flint, 1987; Murray et al., 1989, 1995; Kononov et al., 2005; Başturk et al., 1994; Codispoti et al., 1991; Oguz, 2002). Seasonal variations of the position of this layer ("boundary of life") are rather significant (Bezborodov and Eremeev, 1993), with the maximum depth of hydrogen sulphide being recorded in autumn, the minimum - in spring (Bezborodov, 1988).

In biological oceanography a distinction is made between waters with sufficient ('normal') dissolved oxygen and those with an ecologically significant oxygen deficit. Living conditions in these types of waters are referred to as normo- and hypoxic, respectively. When it was found that the lower tolerance level of benthic organisms in the coastal zone corresponds to oxygen concentrations less than 2 ml.L^{-1} , this value was taken as the boundary between normoxia and hypoxia (Rosenberg, 1980). Deep-sea benthos was later found to be tolerant to concentrations of about 1 ml.L^{-1} (Rosenberg et al., 1991). As a result, the following classification of environments according to bottom-water oxygen content has been proposed (Middelburg and Levin, 2009): normoxic ($>63 \mu\text{M O}_2 \times \text{L}^{-1}$; $> 2 \text{ mg O}_2 \times \text{L}^{-1}$; $> 1.4 \text{ ml O}_2 \times \text{L}^{-1}$); hypoxic ($<63 \mu\text{M O}_2 \times \text{L}^{-1}$; $<2 \text{ mg O}_2 \times \text{L}^{-1}$; $<1.4 \text{ ml O}_2 \times \text{L}^{-1}$); oxygen-free ($0 \mu\text{M O}_2 \times \text{L}^{-1}$); and sulphidic (0 oxygen and free sulfide present). The known response of zoobenthos to hypoxia is a reduction in the number of species and overall density, as repeatedly shown in different waters. Increasing oxygen deficiency modifies animal behaviour, following which the species richness, abundance and biomass of the benthic community gradually decrease. At a certain stage in the development of hypoxia, the bottom sediments become black in colour and have a distinct hydrogen sulphide smell. Current investigations on the Black Sea benthos have focused on coastal communities. For various reasons, researchers generally do not take into account eukaryotic protozoans as components of marine benthic communities. For many years, gromiid and large soft-walled foraminifera ('allogromiids') were considered difficult for non-specialists to taxonomically classify and were even not recognized as protozoans (Gooday et al., 2000b; Nyholm and Gertz, 1973). This was also the case in studies of Black Sea benthic communities. However, in recent years we have obtained extensive data on benthic protozoans as part of the Black Sea meiobenthos. They have been recorded in the meiobenthos along the shelf and continental slope of

the Black Sea in environments with reduced oxygen levels (Brennan et al., 2013; Revkov and Sergeeva, 2004; Sergeeva, 2003, 2016; Sergeeva et al., 2012, 2013, 2015; Sergeeva and Anikeeva, 2014; Sergeeva and Gulin, 2007; Sergeeva and Zaika, 2013; Ürkmez et al., 2015, 2016).

Disturbance of benthic communities and faunal mortality continues until normoxia is restored (Rosenberg et al., 1991). This response to hypoxia is mainly exhibited by the macrofauna. Information on the response of meiobenthos to habitat oxygen depletion is scarce, but it is generalised (Wetzel et al., 2001) that meiofauna are sensitive to prolonged hypoxia, but some adapt to oxygen deprivation for short periods (a few weeks or even months). Generally, some foraminifera and nematodes are most resistant to hypoxia/anoxia (Wetzel et al., 2001). For example, Bernhard et al. (2000) described a remarkably abundant eukaryotic community of protozoans and multicellular meiofauna in the Santa Barbara Basin (California, USA) in oxygen-free and sulphidic sediments.

In recent years, numerous data have been obtained on the spatial and bathymetric distribution of Black Sea meiobenthos, of which soft-walled foraminifers and gromiids are consistent components (Sergeeva et al., 2012, 2013, 2015, 2017). These data have established that there are certain regularities and specific features in the distribution of these protozoan groups. The faunal communities of bottom sediments in the northwestern and southern Black Sea change along a depth gradient from normoxic to different levels of permanent hypoxia and anoxia (Sergeeva et al., 2012, 2013, 2015). Unicellular and multicellular organisms respond in different ways to these environmental changes. In this chapter, using published and new data, we review the distribution of soft-walled foraminifera and gromiids in different areas of the Black Sea according to depth and the oxygen content in bottom waters.

We have very extensive collections of soft-walled foraminifera and gromiids from different parts of the basin, but it will take more than one year for a team of specialists to study the species composition of this material. In order to draw the attention of researchers to the importance of these consistent and numerous components of benthic communities, we provide some data on their bathymetric distribution in the Black Sea, considering only quantitative characteristics. Where appropriate, we compare trends in the distribution of soft-walled monothalamous foraminifera (SWF) and hard-shelled multichambered foraminifera (HSF). Information on the resistance of soft-walled foraminifera of the Black Sea to extreme hypoxia and persistent anoxia with hydrogen sulfide is contained in several of our works (Sergeeva and Gulin, 2007; Sergeeva et al., 2010, 2012, 2017; Sergeeva and Mazlumyan, 2013, 2015).

Four zones have been identified in the Black Sea according to the depth gradient and the oxygen concentration in the bottom waters (Lichtschlag et al., 2015): oxygenic, depths <130 m ($> 63 \mu\text{mol} \times \text{L}^{-1}$), oxygen/hypoxic, depths 130-142 m (> 63 to $> 0 \mu\text{mol} \times \text{L}^{-1}$), hypoxic/oxygen-free, depths 142-167 m ($63-0 \mu\text{mol} \times \text{L}^{-1}$) and oxygen-free/sulphide, depths > 167 m (oxygen-free water contains hydrogen sulfide). Based on the oxygen concentration in bottom water, environmental conditions for meiobenthic organisms along the boundary zone on the outer western Crimean shelf and in the Istanbul Strait area of the Black Sea ranged from normoxic ($175 \mu\text{mol} \text{O}_2 \times \text{L}^{-1}$) to hypoxic (less than $<63 \mu\text{mol} \text{O}_2 \times \text{L}^{-1}$) and anoxic/sulphidic for several kilometres (Holtappels et al., 2011, 2012; Lichtschlag et al., 2015).

The distribution of metazoan and single-celled meiobenthic organisms along this oxygen gradient was investigated in the areas of the Istanbul Strait (Bosporus) and the western shelf of the Crimean Peninsula (Fig. 7.1) (Sergeeva et al., 2017). The aim of these studies was first to understand the response of the main benthic protozoan taxa to oxygen depletion, and secondly, to analyze the change in the contribution of these taxa to the meiobenthos of the Black Sea, both under shallow-water oxygenated conditions and also in the deeper, permanently anoxic environments.

The other important objective of the study was to reveal the poorly-known benthic protozoans of the Black Sea, including Ciliophora, Gromiida and Foraminifera (both hard-shelled multichambered and soft-walled monothalamous), as components of the bottom communities, and to attract the attention of scientists to the necessity for more comprehensive benthic studies in order to assess the significant role of various size- and ecology-related faunal compartments in the functioning of benthic ecosystems in this unique basin. Thus, we focused on the contribution of these taxa to the meiobenthic communities in different regions of the Black Sea, with examples from the oxygenated shelf waters and along the oxic/anoxic interface zone of the upper slope, taking into account certain characteristics (bathymetric and spatial distribution, abundance, and contribution of these organisms to the total meiobenthos). Benthic communities comprise a number of size-related compartments, namely the micro- (10 to 100 μm), meio- (100 to 1000 μm) and macrobenthos (more than 1 mm) (Mare, 1942). In this study we considered all meiobenthic organisms, both protozoans and metazoans including permanent as well as temporary meiobenthos, the latter representing juvenile stages of macrobenthos (Bougis, 1950; Chislenko, 1961; Giere, 2009; Higgins and Thiel, 1988; Luth and Luth, 1997, 1998; Sergeeva, 2004; Sergeeva and Gulin, 2007; Sergeeva et al., 2012, 2013; Soltwedel, 2000).

The changes in the distribution of benthic protozoans and metazoans and the proportion of main benthic protozoan taxa in the deep-water meiobenthos along oxic/anoxic interface (75-300 m) was studied in the outlet area of the Istanbul Strait (Bosporus) and the northwestern region of the Crimean Peninsula (Fig. 7.1A, B).

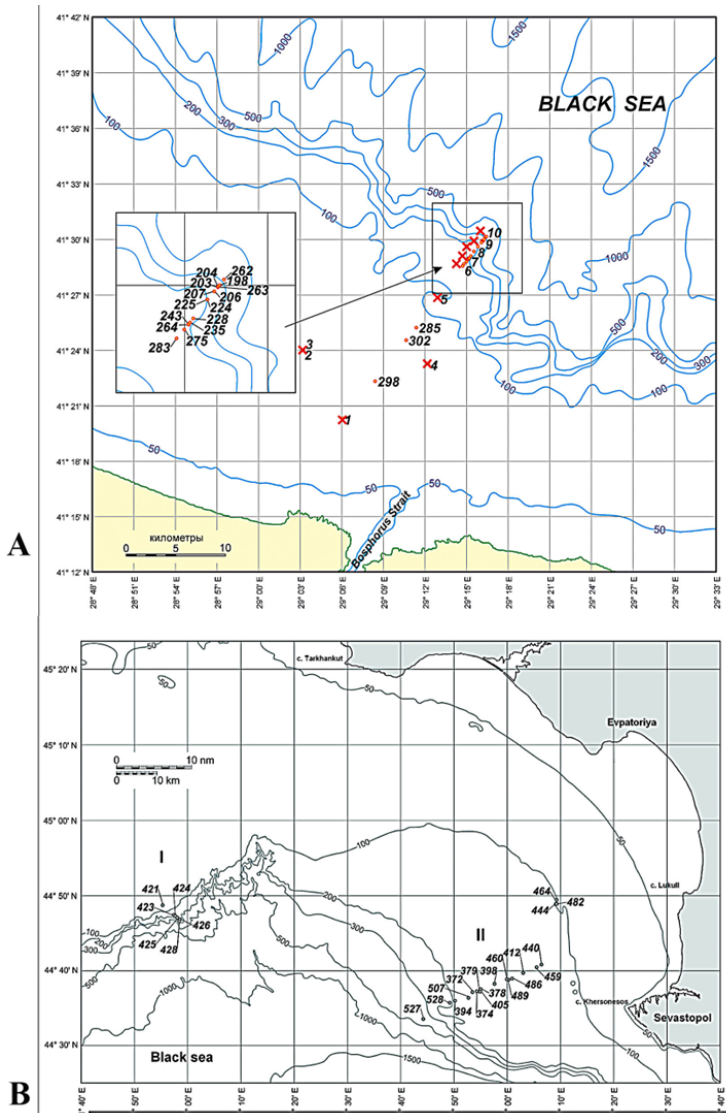


Figure 7.1. Meiobenthic sampling stations at the outlet area of the Istanbul Strait (A) in the Black Sea (Station 1-10 R/V “Arar”, 09.2009, 203-302, R/V “Maria S. Merian”, 04.2010) and at the outer western Crimean shelf (B) located on Area I and Area II (R/V “Maria S. Merian”, 05.2010)

The distribution of Protozoa and Metazoa along the bottom-water oxygen gradient in these areas shows the same general pattern. Protozoans persist as part of meiobenthos up to the last zone (anoxic/sulfidic), but at the same time there are differences in the relative proportions of metazoans and protists, as well as the relative abundance of particular protozoan taxa (Figs. 7.2 and 7.3). At the current stage of investigation of the taxonomic composition of SWF at each depth, we can assume that

anoxia- and hydrogen sulphide-tolerant species, which constitute an appreciable proportion of total meiobenthos, will undoubtedly be distinguished among this group.

Benthic protozoans are characteristic of the entire studied depth range (80-300 m) in the area near the Bosphorus, but their distribution is irregular (Fig. 7.2). The contribution of protozoans to the meiobenthos was 5-12%. The lowest proportion was observed in the oxic zone, and they accounted for at least 6% with increasing depth across the transition to extreme conditions. The occurrence of each of the benthic protozoan taxa over this wide range of depths indicates that soft-walled foraminifers and gromiids constitute a significant proportion of the protist and meiobenthos communities at different depths and at different levels of bottom-water oxygenation.

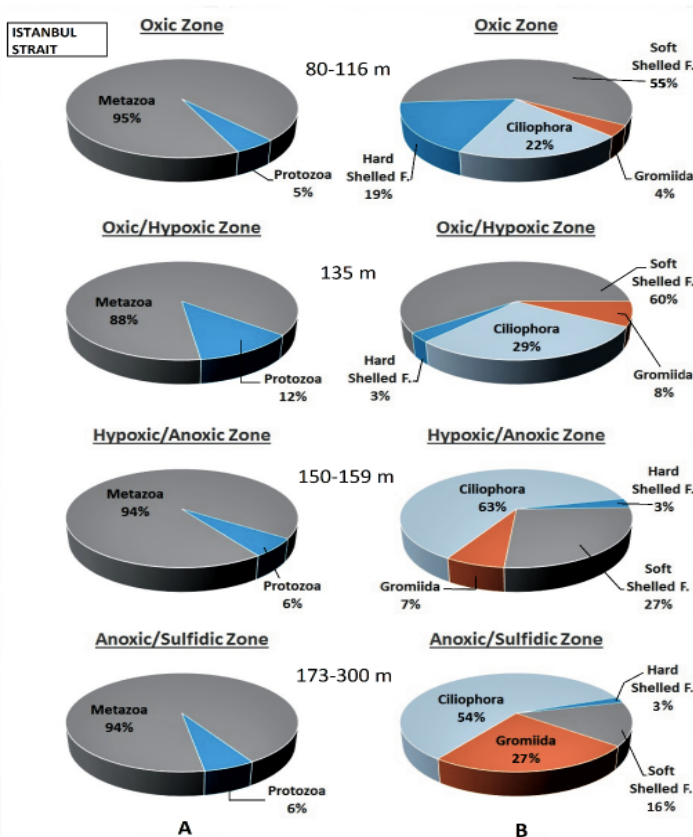


Figure 7.2. Proportions of Protozoa and Metazoa among the total meiobenthos (A), and proportions of major benthic taxa among protozoan communities (B) along the studied depth gradient offshore in the Istanbul Strait (Bosphorus) area (Black Sea, April 2010) (from Sergeeva et al., 2017).

In the region near the Istanbul Strait (Bosphorus), two groups, soft-walled foraminifera and ciliates, make the greatest contribution to protozoan assemblages in terms of abundance, although their relative importance switches with increasing depth. In the first (normoxia) and second (normoxia/hypoxia) zones SWF dominate,

representing 55 and 60% (respectively) of the total abundance of protozoans. In contrast, the proportion of hard-shelled foraminifera is notable (19%) only in the oxygenated zone (80-116 m). Ciliates become dominant with increasing depth and as conditions change from hypoxic to anoxic with hydrogen sulphide, but the proportion of SWF remains significant (27 to 16%).

A surprising pattern in the distribution of gromiids and their contributions to protozoan assemblages along the depth gradient is observed in the Bosphorus area. As shown in Fig. 7.2, gromiids represented the lowest proportion of the total protozoan abundance in normoxic conditions (4%); their proportion increased to 7-8% as depth increased and, consequently, bottom-water oxygen decreased, while in permanently anoxic conditions they reached 16%. There is currently no explanation for this pattern.

The region of the Istanbul Strait (Bosphorus) has a complex hydrological regime. Salt water from the Marmara Sea enters the Black Sea through the Istanbul Strait (Bosphorus) at all seasons of the year. In the shallow areas, this water mass can be traced as a clear stream at a depth of 80-100 m. Environmental conditions are modified here by the influence of this saline and normoxic water, possibly leading to a shift of the oxygenated water boundary to greater depths. On the continental slope, the Marmara Sea water moves away from the bottom and is entrained by the general flow of the Black Sea waters to the north-east and east (Özsoy and Ünlüata, 1997).

It is possible that these complex processes of mixing waters of Marmara and Black Sea occurring in the area near Bosphorus periodically deliver at least a minimal amount of oxygen benthic protozoans and meiobenthos living in deep-water habitats. However, it is difficult to accept that benthic organisms with different physiological adaptations are capable of rapidly rearranging their metabolic mechanisms when the oxygen regime changes. Rather, this may serve as a stressor and cause organisms to die.

The claims of some scientists that benthic organisms originate from the upper oxygen horizons and are subsequently preserved in a sulphidic environment are, in our opinion, untenable. It is very difficult to explain the selectivity of these inputs, namely that only certain groups of protozoans and some small meiofaunal animals with delicate soft bodies lacking hard protective structures reach extreme depths without disrupting their integrity. Secondly, alive protozoan and metazoan species that were previously unknown have been found in the anoxic and sulphidic environment of the Black Sea (Sergeeva, 2003, 2004; Korovchinsky and Sergeeva, 2007; Sergeeva et al., 2014). This convinces us that SWF and other organisms that possess specific adaptations to toxic conditions are found here in their natural environment.

Thus, we tend to believe that the ratio of the main groups of benthic protozoa, including SWF, is characteristic of meiobenthos in the studied depth range near the Bosphorus. However, it should be noted that SWF may not have been fully documented since those with long, thin tests (genus *Nemogullmia*, some *Tinogullmia*) often disintegrate during mechanical processing of bottom sediments samples.

The southwestern Crimean shelf differs greatly from the area near the Bosphorus in terms of deep-water benthic habitat. A study of the bathymetric distribution of meiobenthos, including protozoans, was carried out in two polygons (Fig. 7.1, I and II). Using a remote sensing device "Medusa", German colleagues surveyed the seafloor in the study areas, revealing a heterogeneous biotope structure and the mosaic

colouring of the substrates, as well as the presence or absence of ferromanganese nodules and bacterial mats. Four zones from normoxia to anoxia/hydrogen sulfide were identified in terms of the oxygen gradient.

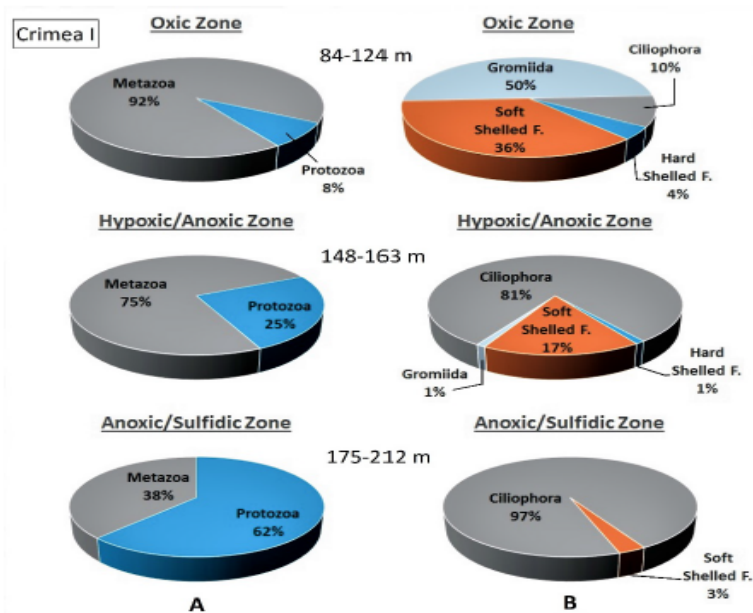


Figure 7.3. Proportions of Protozoa and Metazoa among the total meiobenthos (A) and proportions of major benthic taxa among protozoan communities (B) along the studied depth gradient in the western Crimean shelf, Polygon I (May 2010) (from Sergeeva et al., 2017)

The proportion of protozoan in the meiobenthos increases as bottom-water oxygen decreases towards the extreme environment. Their contribution in polygon I increases from 8% in normoxic to 62% in anoxic/sulphidic waters (Fig. 7.3). The proportion of SWF (36%) decreases in the same direction, from 36% in the oxic to 3% in the anoxic/sulphidic zone, while gromiids account for 50% of the total protozoan abundance in the oxic zone but only 1% where conditions are hypoxic, below which they are absent. The overall increase in the proportion of protozoans with depth is therefore attributable to the ciliates, which increase from 10% to 81-97% of the protozoa.

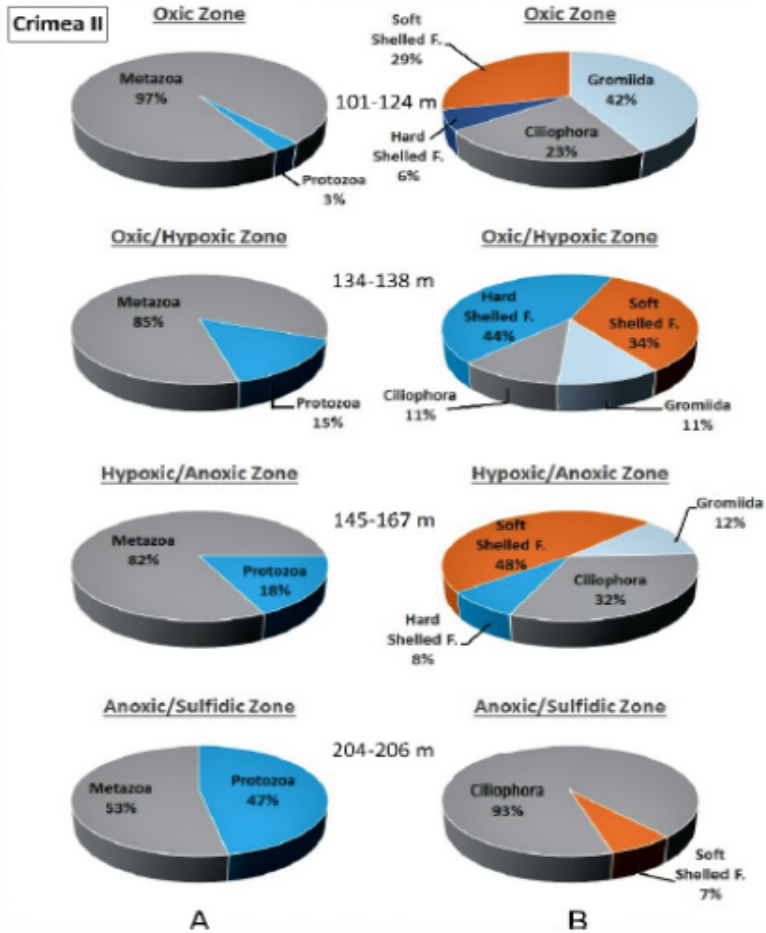


Figure 7.4. Proportions of Protozoa and Metazoa among the total meiobenthos (A) and proportions of major benthic taxa among protozoan communities (B) along the studied depth gradient in the western Crimean shelf, Polygon II (May 2010) (by Sergeeva et al., 2017)

In summary, the following conclusion can be drawn regarding the distribution of protozoans, in particular SWF, along depth and oxygen gradients in the Black Sea. Soft-walled foraminifera, and the protozoan community in general, show a tolerance to a deficiency or lack of oxygen in the habitat. Their quantitative development, together with changes in oxygen concentration and the occurrence of hydrogen sulfide in the environment, is greatly influenced by other associated biotic and abiotic factors (bioturbation, granulometry, bacterial mats, trophic resources, etc.).

CHAPTER 8

BENTHIC PROTOZOANS AS A COMPONENT OF THE DEEP-WATER BLACK SEA MEIOBENTHOS

Benthic protozoans, Foraminifera (hard- and soft-shelled), Gromiida, and Ciliophora, are widespread and numerous in the Black Sea and the Sea of Azov. Long-term studies of the Black Sea meiobenthos has provided extensive information on their diversity, spatial and bathymetric distribution, and their contribution to the structure of benthic communities (Vorobyeva, 1999; Sergeeva, 2003; Revkov and Sergeeva, 2004; Sergeeva and Gulin, 2007; Sergeeva et al., 2012, 2017; Sergeeva and Anikeeva, 2014; Sergeeva and Mazlumyan, 2015). Protozoa, together with multicellular organisms, are an important component of benthic communities, often accounting for a significant proportion of the total benthic fauna. In the previous section, the bathymetric distribution of these four groups of protozoans, and changes in their relative abundance with increasing depth (75-300 m) across zones where oxygenated and sulphidic water masses mix, was demonstrated based on examples from the shelves of Türkiye and the Crimea. It is obvious that the contribution of soft-walled foraminifera to meiobenthic communities in different parts and biotopes of the Black Sea must be considered. Some data have already been published (Sergeeva and Anikeeva, 2014; Sergeeva and Mazlumyan, 2015; Sergeeva et al., 2012, 2013, 2015, 2017). Here we present more detailed information on the distribution of SWF abundance in some open coastal areas and bays near Sevastopol.

8.1. Open Sea

8.1.1. Istanbul Strait (Bosporus) area of the Black Sea (Turkish shelf)

The vertical distribution of soft-walled foraminifera along the depth gradient in the area of the Istanbul Strait (Bosporus) was studied during the autumn and spring based on samples collected during two cruises of the 'Arar' (ITU) in November 2009 and the 'Maria S. Merian' in April 2010 (see Fig. 7.1). The depth distribution was very different during these two periods (Figs. 8.1; 8.2). In both cases, peaks in the quantitative development of monothalamous foraminifers (SWF) and multi-chambered foraminifers (HSF) were observed. The following points are noteworthy: (1) the presence of two or more peaks within the range of depths studied, (2) differences in the depths where SWF and HSF density peaks are observed, (3) differences in the timing of peaks at different depths.

In 2009, the abundance of meiobenthos tended to decrease with depth, but the decrease was uneven (Fig. 103). There were several peaks, the two larger of which were located at depths of 75 m (about 1800×10^3 ind./m²) and 88 m (a little more than 1 million ind./m²) in the oxic zone. These were followed by two smaller peaks at 160 m (469×10^3 ind./m²) and 250 m (more than 602×10^3 ind./m²) in the anoxic/sulfidic zone. Visual assessment of sediments in multicores revealed a change from dense oxidized silt at depths of 75-100 m to black silt starting from 122 m depth. The surface of the black silt was covered by a thin brown film (bacterial?) only at the 160-m station. At the next three stations (190-300 m) the sediment was black with a soft sludge-like consistency and a distinct hydrogen sulfide smell.

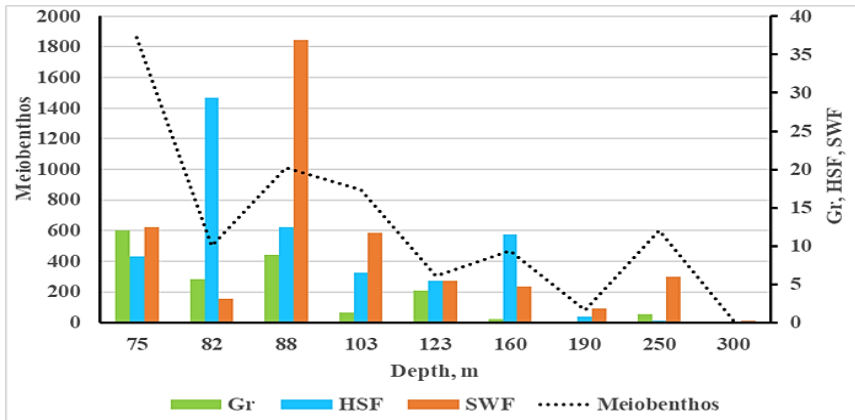


Figure 8.1. Density ($N \times 10^3 \text{ ind./m}^2$) of protozoans and meiobenthos as a whole in the transition zone from normoxia to hypoxia and anoxia associated with hydrogen sulfide along a depth gradient in the Istanbul Strait (Bosporus) region (R/V “Arar”, November, 2009): *Gromia* (Gr), hard-shelled Foraminifera (HSF) and soft-walled Foraminifera (SWF).

SWF were found throughout the studied depth range (75-300 m). There was a general trend of decreasing density with depth, but with a sharp peak of SWF abundance ($37 \times 10^3 \text{ ind./m}^2$) at a depth of 88 m. In anoxic environments with hydrogen sulfide at depths of 250 m and 300 m, the densities of SWF were $6 \times 10^3 \text{ ind./m}^2$ and 300 ind./m^2 , respectively. Most were associated with detritus and the upper 0-2 cm sediment layer. The species *Goodayia rostellata*, *Tinogullmia* sp., and *Nemogullmia* sp. were most common in hypoxic and anoxic conditions, suggesting that they have a tolerance to hydrogen sulfide (Sergeeva and Mazlumyan, 2013; present).

Hard-shelled as well as soft-walled foraminifera were recorded to a depth of 250 m. Their density was greatest (about $30 \times 10^3 \text{ ind./m}^2$) at 82 m depth, with two smaller peaks ($12-13 \times 10^3 \text{ ind./m}^2$) at the 88 m and 160 m sites, which have sharply different habitat characteristics. At depths of 190-250 m the density of HSF is minimal (not more than 1 thousand ind./m^2) and they were absent at 300 m. HSF represented 5.90% of the total meiobenthic density at a depth of 82 m. Their contribution became insignificant with increasing depth, apart from a secondary peak of 2.44% at a depth of 160 m in hypoxic conditions. The most abundant species of HSF is *Hyperammina* sp., which has a brittle test composed of sand-sized particles and reaches a size of more than 3 mm. We considered this to be part of the macrobenthos (Sergeeva and Mazlumyan, 2013). Two other HSF species, *Ammonia compacta* Hofker, 1964 and *Eggerella scabra* Williamson, 1858, were abundant.

The maximum densities of gromiids ($12,500-10,000 \text{ ind./m}^2$) were confined to the oxygen zone in November 2009, but they occurred in smaller numbers down to a depth of 250 m (Fig. 8.1) A different trend was found in the distribution of gromiids in April of the following year (Fig. 8.2).

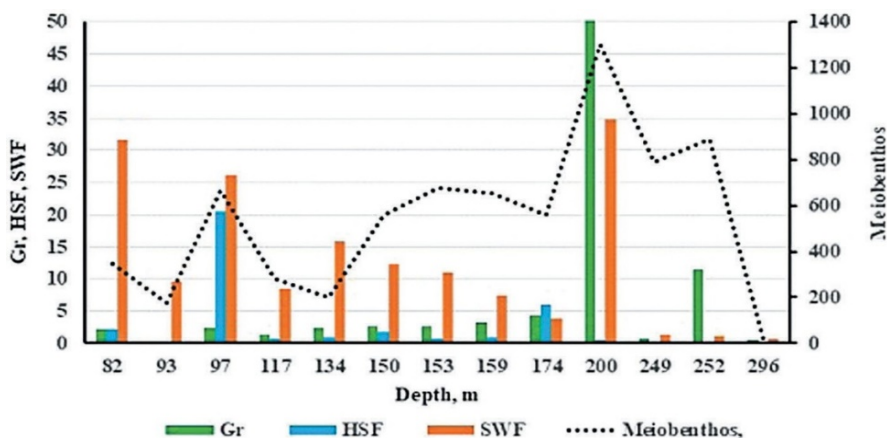


Figure 8.2. Density ($N \times 10^3 \text{ ind./m}^2$) of meiobenthos as a whole, *Gromia* (Gr), hard-shelled Foraminifera (HSF) and soft-walled Foraminifera (SWF) in the zone the transition from normoxia to hypoxia and anoxia and sulfidic along depths gradient in the Istanbul Strait (Bosporus) region (R/V “Maria S. Merian”, April, 2010)

In general, the contribution of foraminifera (SWF and HSF) to the total density of meiobenthos at stations confined to normoxic conditions was up to 6% (88 m), in hypoxic/anoxic conditions 3.5% and in anoxic/sulfidic environments 2.8%. Soft-walled foraminifers occurred at all surveyed depths are part of the meiobenthos, but their contribution to its total meiobenthic density during this period did not exceed 3.7% (88 m depth). Slightly lower proportions, 2.80 and 2.50%, were observed in anoxic and sulfidic habitats (300 m and 190 m depths).

In spring 2010, the quantitative distribution of meiobenthos and its protozoan components had unexpected characteristics. Meiobenthos densities along the depth gradient ranged from 18×10^3 (296 m depth) to $1.5 \times 10^6 \text{ ind./m}^2$ (200 m depth). Notably, the density of meiobenthic communities in normoxic conditions at depths of 82, 93, 117 m ranged from 187 to $381 \times 10^3 \text{ ind./m}^2$, which was comparable with values for hypoxic environment (134 m), whereas densities at the 97 m isobath exceeded $700 \times 10^3 \text{ ind./m}^2$. Even more surprisingly, the density did not follow the expected decreasing trend with depth but peaked in the extreme anoxic/sulfidic at 200 m depth (to $1.5 \times 10^6 \text{ ind./m}^2$) with a second noticeable spike at 250 m depth ($903 \times 10^3 \text{ ind./m}^2$).

Other features were observed in the distribution of SWF and HSF. Both groups of foraminifera showed a clear tendency to decrease in abundance along depth and oxygen gradients. Densities of soft-walled foraminifers were $31.5 \times 10^3 \text{ ind./m}^2$ at a depth of 82 m, following which their abundance decreased sharply at 93 m before reaching a second peak at 97 m (more than $26 \times 10^3 \text{ ind./m}^2$). There was a smooth decrease in abundance down to 174 m depth, but at 200 m, SWF showed their maximum development (34.800 ind./m^2) in the transect. Below this depth, the number of monothalamids decreased sharply to $1.4 \times 10^3 \text{ ind./m}^2$ (250 m) and 700 ind./m^2 (296 m). Thus, SWF in the Black Sea inhabit a wide range of depths, including a zone of constant hypoxia/anoxia with hydrogen sulfide, albeit with an uneven bathymetric distribution.

Some species, such as *Bathyallogromia* sp., were found at 130 m depth (Sergeeva et al., 2010), and *Tinogullmia* sp. and *Psammophaga* sp. – at depths of 150–160 m (Sergeeva et al., 2010). *Goodayia rostellata*, three morphospecies of the genus *Vellaria*, and *Nemogullmia* occur in the Black Sea deeper than 150–250 m, where benthic water is sharply hypoxic and sulphidic.

The greatest contribution (5.15–8.30%) was made by SWF to the meiobenthos of the oxic zone, whereas under hypoxic (134 m) and anoxic (296 m) conditions they accounted for 7.20 and 3.64%, respectively. The total contribution of foraminifera (HSF and SWF) to meiobenthos numbers reached 7.2–9%.

The population density of gromiids along the depth gradient during the spring period did not differ significantly, but where conditions were severely hypoxic and sulfidic at a depth of 200 m, there was a surge in their numbers (65×10^3 ind./m²) that exceeded those of all other protozoans.

It should be noted that significant differences between the 2009 and 2010 samples were found in other groups of meiobenthos (Zaika and Sergeeva 2008, 2009, 2012; Sergeeva and Mazlumyan, 2013; Sergeeva et al., 2008; Kolesnikova et al., 2014).

Small numbers of HSF were recorded but only down to 200 m depth. Their maximum density (20.5×10^3 ind./m²) was in the oxygenated environment at a depth of 97 m. HSF abundance at other depths varied from 350 ind./m² (200 m) to 6×10^3 ind./m² (174 m).

Data on the ability of SWF and HSF to penetrate the sediment profile was obtained from multicorer samples collected during the autumn 2009 and spring 2010 cruises. Each core was sliced into 1-cm layers from the surface to 10 cm depth, although we limited our analyses of foraminiferal assemblages to the upper 5 cm (five layers). This method was applied previously to reveal the vertical distribution of meiobenthos within the sediment at different sites (Sergeeva et al., 2013, 2015; Sergeeva and Zaika, 2013). The depth to which oxygen penetrates the sediment in the normoxia zone is shown in Fig. 8.3.

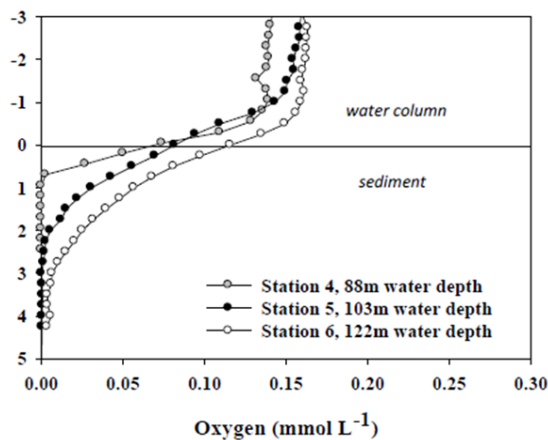


Figure 8.3. Oxygen concentrations in bottom sediments and bottom water of the normoxia zone at three stations in the area of the Istanbul Strait (Bosporus) in autumn 2009 (by A. Lichtschlag in Sergeeva et al., 2013)

In autumn 2009, HSF did not penetrate deeper than 4 cm (3-4 cm layer) at depths of 75-82 m, while at 88 m depth they were only found down to 3 cm (2-3 cm). At 190 and 250 m depth, HSF were absent at the surface, but isolated individuals were found in layers 2 and 3 cm. SWF were generally found in the layers 1 – 2 cm layer at all sites, and at depths of 88 - 123 m, and 190 and 250 m they were often recorded down to 3 and 4 cm. In addition, SWF were observed in the surface layer at 300 m. This suggests that monothalamids are more resistant to hypoxia than HSF (Sergeeva et al., 2015).

Based on the material from the April 2010 RV 'Maria S. Merian' cruise collected in the same area, HSF were found down to 2 cm only at depths of 75 m and 97 m. SWF were consistently present in the surface layer and usually also in the 1-2 cm layer, even at depths of 300 m. They were found at all the stations and in more layers than HSF, although not in layer 4 (3-4 cm) at the 135-m site (Sergeeva et al., 2015). These samples therefore support the conclusion that monothalamids have greater tolerance to hypoxia than HSF.

Comparing the results of the two surveys, a decrease in the number of HSF throughout the area between the two investigations is remarkable. At the same time, the abundance of SWF slightly increased and this group of foraminifera was recorded in small numbers even at a depth of 300 m. These differences, as well as the differences observed in other meiobenthos groups, are obviously related to fluctuations in the downstream Bosphorus current, which affects not only meiobenthos but also macrobenthos.

Macrobenthos are found in this area at much greater depths than in other regions, and this is also due to the influence of water flow from the Istanbul Strait (Bosphorus) (Sergeeva et al., 2011, 2014). As a result, the sediment is more deeply bioturbated, increasing the depth of oxygen penetration and therefore the depth to which meiobenthos, and foraminifera in particular, penetrate. This leads to an increased abundance of protists that are adapted to such conditions.

8.1.2. North-western part of the Black Sea (southwestern shelf of Crimea)

The foraminifera on the western shelf of the Crimean Peninsula were analysed, based on cores collected in two polygons during the May 2010 'Maria S. Merian' cruise. Six stations in polygon I covered depths of 84-212 m, while the depth range on polygon II was 101-375 m. In each case, foraminifera were not observed at the deepest sites (212 and 375 m).

During the study period, the oxygen concentration in the near-bottom water varied over a wide range, changing from normoxia ($175 \mu\text{mol O}_2 \times \text{L}^{-1}$) to hypoxia ($<63 \mu\text{mol O}_2 \times \text{L}^{-1}$) and even to anoxia with hydrogen sulfide. Variations in oxygen concentrations between 160 and $10 \mu\text{mol O}_2 \times \text{L}^{-1}$ occurred over periods as short as several hours near the chemocline at a depth of 134 m. The effect of these fluctuations on the biota in the bottom sediments of this area has been studied in detail (Lichtschlag et al., 2015).

The bottom sediments within the polygons are not homogeneous. Before sampling, observation of the surface structure and bottom topography, distinctive features of fauna habitats etc. were carried out using a laser scanning device (LS) and a high-resolution MEGACAM camera, installed on a mobile benthic crawler (MOVE, MARUM, Bremen). This overview revealed faunal heterogeneity, the presence of

bacterial mats in some areas, differences in bottom surface colouration and other characteristics.

The distribution of foraminifera along a bathymetric gradient in this region has been described previously (Sergeeva et al., 2015). It was noted that in April 2010 in polygon II, SWF and HSF had sharp peaks in abundance at 138 m depth, with soft-walled foraminifera having a much higher density (240×10^3 ind./m²) than hard-shelled foraminifera (154×10^3 ind./m²). Both groups also showed small peaks at depths of 155-163 m. Multi-chambered foraminifera (HSF) occurred in minimal numbers at a depth of 167 m, while monothalamids (SWF) were present at a depth of 204 m.

Here we consider the quantitative distribution of these groups of foraminifera in the two polygons, how they relate to each other and how they contribute to the total abundance of meiobenthos. We considered it important to show the spatial distribution of foraminifera without averaging their quantitative characteristics if they fall within the same depths. This reveals how the variability in their abundance, including the relative abundance of SWF and HSF, is influenced not only by the oxygen concentrations along the depth gradient, but also by other factors that we are not yet able to measure.

In polygon I, SWF abundance varies along the depth gradient and follows a similar pattern to that of the metazoan meiobenthos (Fig. 8.4). Maximum SWF abundance peaks at 148 m depth, where conditions are hypoxic/anoxic, with smaller peaks in the normoxic zone at 84 m depth. HSF represent only 0.2-0.4% of meiobenthos and only occur down to a depth of 163 m, whereas SWF account for 3.2-2% of total meiobenthos in oxygen conditions (84-124 m), 3.6-4.2% in hypoxia/anoxia conditions (148-163 m) and in anoxia with hydrogen sulfide (175 m).

The greatest abundance of gromiids was observed in the oxic zone (84-124 m), below which their abundance decreased sharply with increasing depth (Fig. 8.4).

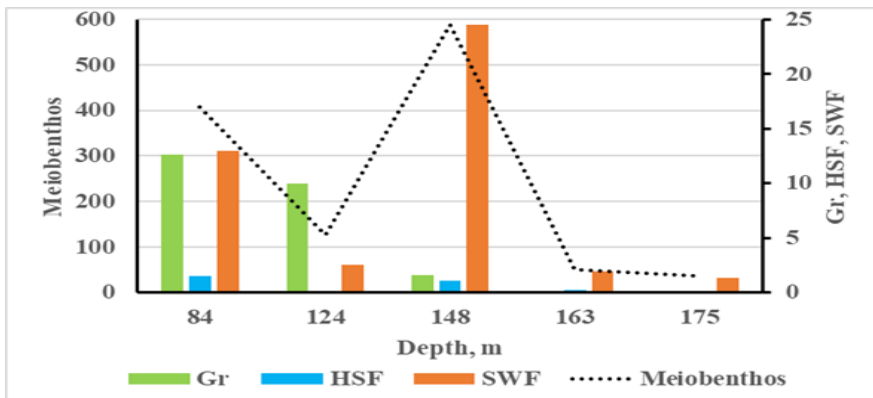


Figure 8.4. Density ($N \times 10^3$ ind./m²) of meiobenthos as a whole, *Gromia*, HSF and SWF in the zone of transition from normoxia to hypoxia and anoxia associated with hydrogen sulfide, on the western shelf of the Crimea, polygon I (R/V “Maria S. Merian”, 05.2010)

The distribution of metazoan meiobenthos, SWF and HSF in polygon II is not as consistent as in polygon I (Fig. 8.5). Meiobenthic density was highest in the oxic zone

(range 940×10^3 to 2734×10^3 ind./m²), maintained high values in the normoxic/hypoxic zone (134 and 138 m depths) (over 1500×10^3 and about 2400×10^3 ind./m²) but decreased at deeper sites. The distribution of SWF showed an opposite trend, with low abundances where conditions are normoxic, followed by noticeable increases along the depth gradient and an abundance peak (more than 240×10^3 ind./m²) at a depth of 138 m, coinciding with that of the metazoan meiobenthos. With increasing depth, the SWF density also remained significant in hypoxic/anoxic conditions. HSF were found at all depths except 204 m. They occurred in small numbers where conditions were normoxic, but at the edge of the oxygen zone and within the normoxia/hypoxia zone an increase in values was observed (11×10^3 – 154×10^3 ind./m²). Gromiids occurred in low densities and varied insignificantly with depth in this polygon.

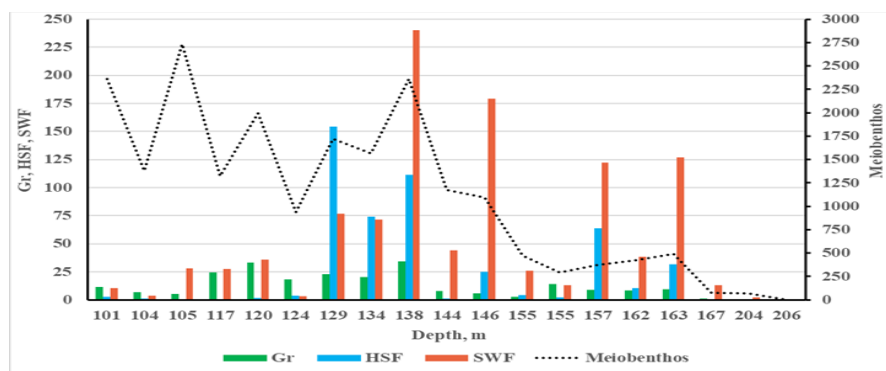


Figure 8.5. Settlement density ($N \times 10^3$ ind./m²) of meiobenthos as a whole, Gr, HSF and SWF in the transition from normoxia to hypoxia and anoxia accompanied by hydrogen sulfide, on the western Crimean shelf, polygon II (May 2010, R/V "Maria S. Merian")

The contribution of HSF to meiobenthos as a whole in polygon II is 0.1- 6.1%, while for SWF it varies from 0.7 to 18.3%. When both groups are combined, they account for 23% of the meiobenthos, with the highest contribution being recorded in the deepest, extreme environment.

The data from these two areas in the northwestern Black Sea reflect changes in the quantitative development of foraminifera along a depth gradient and their abundance peaks in unfavourable habitats. These peaks indicate that foraminifera are found in their optimal environments. This is particularly true for species and other groups of organisms that form a "settlement belt" within a limited depth range (Sergeeva and Zaika, 2000; Zaika and Sergeeva, 2012). A relatively high abundance of foraminifera in hypoxic conditions has previously been noted (Sergeeva and Anikeeva, 2014; Sergeeva et al., 2013). It is possible that some species of foraminifera living in such extreme environments may have the ability to use nitrates under anoxic conditions. The assumption of "nitrate respiration" in foraminifera inhabiting anaerobic conditions has been made by several authors (Bernhard and Reimers, 1991; Risgaard-Petersen et al., 2006; Piña-Ochoa et al., 2010; Koho and Piña-Ochoa, 2012; Glock et al., 2019).

According to the data reviewed above, metazoan meiobenthic densities in the transition zone of the Black Sea, characterized by oxygen deficiency and at greater depths by its absence, reach significant values similar to and even exceeding those in the upper and middle parts of the sublittoral zone. In general, the same trend was observed for soft-walled foraminifera. Obviously, the massive development of some benthic organisms, particularly SWF, in the sublittoral zone of the Black Sea is due to favourable trophic conditions in the bottom sediments and the absence of competitors for food. The trophic requirements of meiofauna are determined not only by the degree of accumulation and transformation of organic matter coming from the water column into bottom sediments, but also by the development of a huge biomass of microflora. For example, Yu.I. Sorokin (1982) noted a maximum total microfloral abundance and the greatest activity of individual taxa in bottom sediments of the Black Sea slope at depths of 100-300 m. The total number of bacteria here, according to his calculations, amounts to 1-5 billion per gram of crude sediment. Such values for total bacterial abundance and biomass are close to those found in the upper sediment layer of mesotrophic or even eutrophic waters. The data presented above on the bathymetric distribution of protozoa, including soft-walled foraminifera, indicate that they undoubtedly form a link to higher trophic levels.

A further detailed study of the species diversity of soft-walled foraminifera and the distribution of species in relation to the oxygen and sulphide regime in the Black Sea will enable the identification of specific groupings of species: anoxybionts (typical anaerobes) living only in an anaerobic environment and facultative anoxybionts and microaerophiles typical of redox and oxidative conditions. The diverse range of habitats, favourable trophic conditions, almost complete absence of competition from macrobenthos, and adaptive capabilities of meiofauna to occupy free biotopes that are unfavourable for other benthic organisms, stimulate the strong quantitative development of meiobenthos.

Soft-walled foraminifera were recorded throughout the depth range investigated and comprised a significant part of the total density of meiobenthic communities. In general, with the observed trend of decreasing HSF and SWF abundance along the depth gradient, there is no clear pattern of change in abundance with depth. It is evident that foraminiferal densities are caused by a number of environmental factors that are not yet fully understood.

8.1.3. North-eastern part of the Black Sea (region Caucasus)

We used an opportunity provided by colleagues from the Institute of Oceanology of the Russian Academy of Sciences (Moscow) to study taxonomic diversity of multicellular and unicellular meiobenthos, its distribution along the gradient of depth and dissolved oxygen across the boundary of the oxyphilic zone of the north-eastern part of the Black Sea (Caucasus area). The study is supported by the RFBR and the Krasnodarsky Region Ministry of Education, Sciences and Youth Policy via the joint research [grant number 19-45-230012].

The study covered two polygons, differing in bottom topography and sediments. The first area is the Golubaya Bay (87-144 m). The second region is the area off Cape Malyi Utrish (82-194 m depth) (Fig. 8.6).

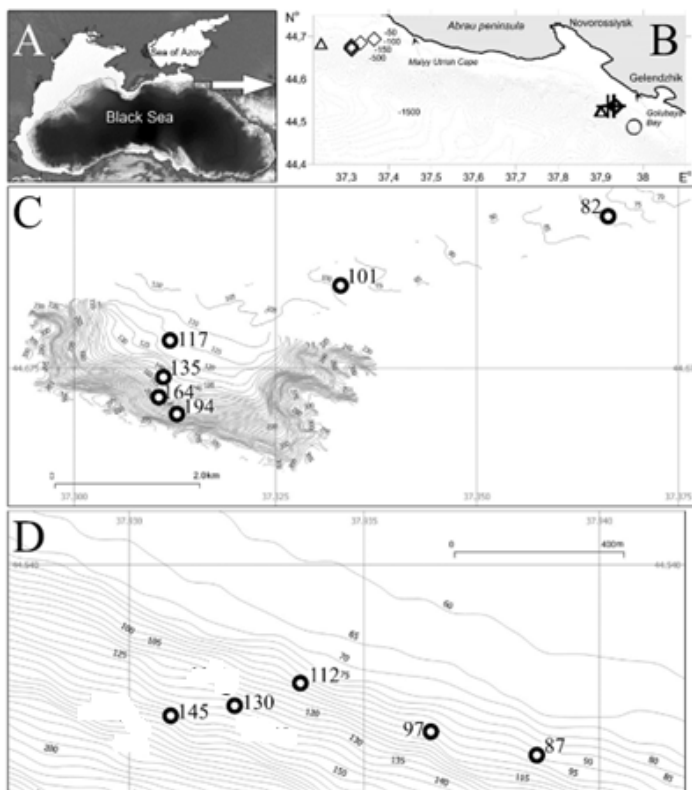


Figure 8.6. Region of study (A); overall scheme of transects (B); bathymetric maps with benthic stations: the area of Golubaya Bay (C), the area of Malyi Utrish Cape (D). (After Kolyuchkina et al., 2022)

At the depths surveyed in the Blue Bay area, the bottom sediments were represented by silty sand with large amounts of plant detritus. In the Utrish Cape area, the bottom sediments were dominated by shells, with the majority of the shells being those of bivalves in the genus *Dreissena*, which inhabited the area more than 7,000 years ago (Kolyuchkina et al., 2019). Earlier publications devoted to the study of benthic communities of the narrow north-eastern Crimean shelf area don't include information on meiobenthos and benthic protozoa in its composition (Kolyuchkina et al., 2019).

Despite the close depth interval between the sampling sites, the quantitative distribution of metazoan meiobenthos and benthic protozoa differed significantly. Meiobenthos abundance ($260\text{--}343 \times 10^3 \text{ ind./m}^2$) in the Malyi Utrish Cape area was only weakly dependent on depth in the range 80–135 m (Fig. 8.7). Protozoa were observed down to a depth of 135 m, but the absence of gromiids in the meiobenthos and the extremely low quantitative HSF values were surprising (Figs. 8.7; 8.8). Hard-shelled foraminifera were only observed in small numbers at 82 m and 101 m, while soft-walled foraminifera ranged from $13 \times 10^3 \text{ ind./m}^2$ to $48 \times 10^3 \text{ ind./m}^2$ and decreased with depth.

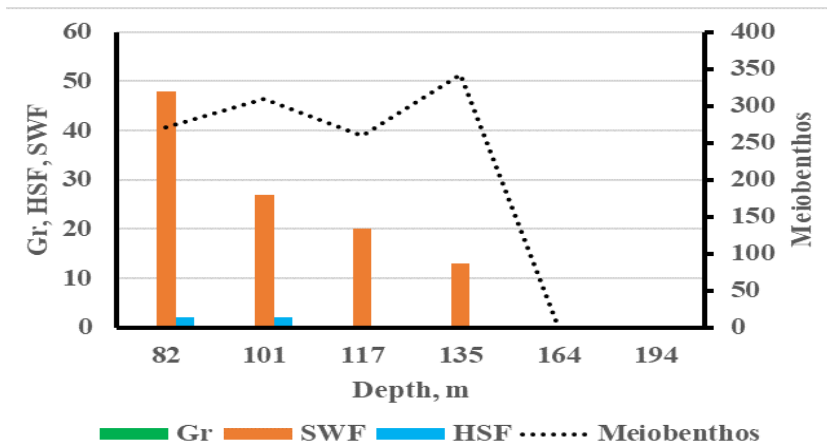


Figure 8.7. Abundance ($N \times 10^3$ ind./m²) of protozoans and meiobenthos as a whole at the depth gradient in cape M. Utrish (2019)

A very different pattern was observed in the bathymetric distribution of benthic protozoa and their contribution to the meiobenthic communities of Golubaya Bay (Fig. 8.8). Meiobenthic densities were several times higher here, but varied noticeably ($207 \times 10^3 - 975 \times 10^3$ ind./m²) at different depths. Moreover, meiobenthic taxa were not detected at 144 m. This is difficult to explain but possibly connected with the small volume of material at our disposal, or perhaps with the anoxic conditions prevailing this site (Kolyuchkina et al., 2019).

In the Golubaya Bay, only 1100 ind./m² gromiids were found at a depth of 112 m, and hard-shelled foraminifers were noted at 87–130 m, also in small numbers (1100–6400 ind./m²). As a result, these groups accounted for only a fraction of a percent of the total abundance of meiobenthos. In contrast, soft-walled foraminifera reached great abundance at depths of 87 and 130 m (205×10^3 and 238×10^3 ind./m²), constituting 20% and 80% of the total meiobenthos abundance, respectively (Fig. 8.8).

Undoubtedly, the variability observed in the quantitative development and taxonomic structure of meiobenthos of these regions is related to the heterogeneity of environmental conditions. The results obtained indicate the importance of taking protozoans into account in assessment of the functioning of benthic communities.

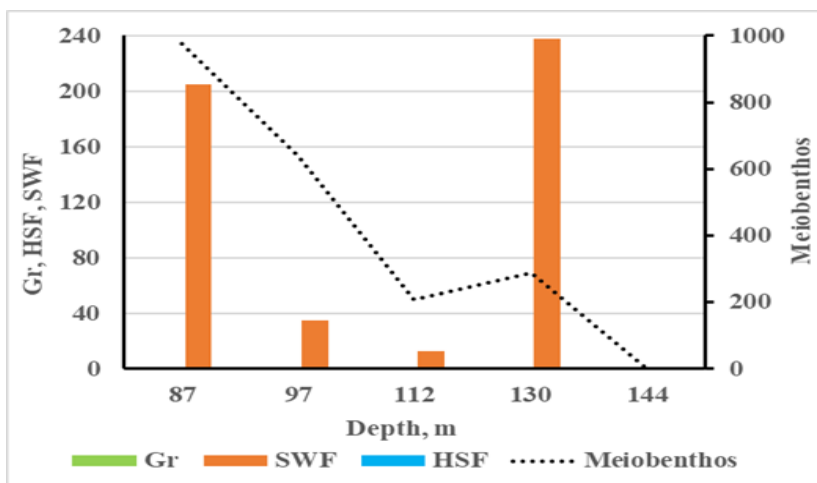


Figure 8.8. Abundance ($N \times 10^3 \text{ ind./m}^2$) of protozoans and meiobenthos as a whole at the depth gradient in Golubaya Bay (2019)

8.1.4. Shelf zone along the Crimean Peninsula (the Black Sea)

The taxonomic composition and distribution of meiobenthos on the Black Sea shelf along the Crimean coastal zone were studied using data from the 64th cruise of the R/V “Professor Vodyanitsky” (07.2010). Benthic sampling was conducted at 13 stations situated along five transects and covering a depth range of 30-192 m (Fig. 8.9).

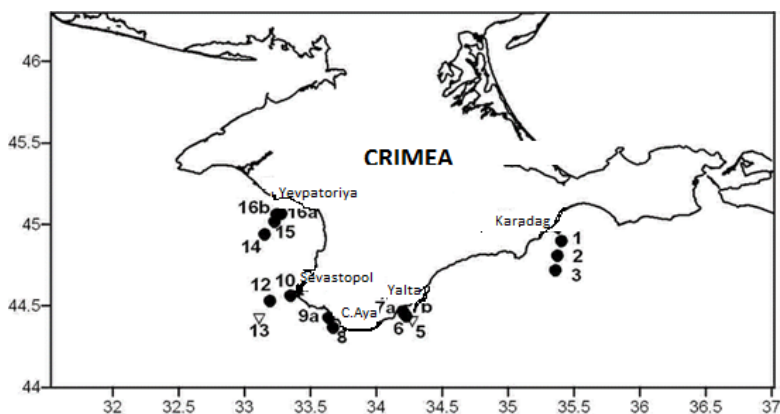


Figure 8.9. Benthic stations along the Crimean shelf (64 cruise R/V “Professor Vodyanitsky”, 06-07.2010)

There is no uniform pattern in the quantitative distribution of meiobenthos and, in particular, foraminifera as a function of depth in each region (Fig. 8.10). At a depth of 72 m in the protected area of the Karadag (I), the density of total meiobenthos and soft-walled foraminifera was not high, but its peak was the same for both groups (136×10^3 and $19 \times 10^3 \text{ ind./m}^2$ respectively). The proportion of SWF as part of the total

meiobenthos at this 72-m station amounts to 14%, decreasing to about 11% at 91 m depth in the open area and 9% at the shallower 48-m station. HSF are recorded only at a depth of 72 m (4%).

In the area of Yalta (II), which is subject of a high recreational impact, three stations (5-7) were investigated at depths where contamination by urban wastewater entering through the deep-water outlet header is possible. At a depth of 192 m no HSF or SWF were detected. At the two stations where foraminifera did occur (84 m and 95 m), the SWF contribution to total meiobenthos was 4.7% and 5.5%, respectively. The highest abundance of total meiobenthos (300×10^3 ind./m²) and SWF (14×10^3 ind./m²) in this area was recorded at the 84-m station.

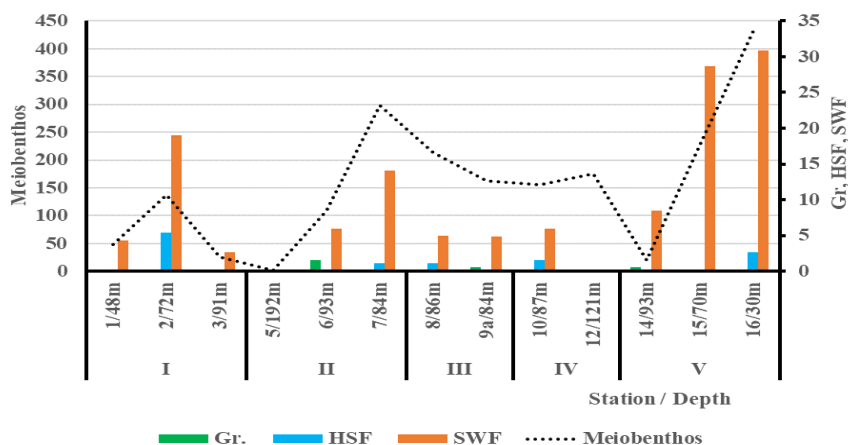


Figure 8.10. Abundance ($N \times 10^3$ ind./m²) protozoans and meiobenthos as a whole along Crimean shelf (cruise 64 of R/V “Professor Vodyanitsky”, 07. 2010)

In the areas of Cape Aya (III) and the Sevastopol area (IV), SWF were not common and represented only a small proportion (2.3-3.8%) of the total meiobenthos. Further west, in the Yevpatoriya area (V), the quantitative development of meiobenthos and soft-walled foraminifera was much greater than in the other study areas along the Crimean coast. Densities of total meiobenthos reached 230×10^3 - 430×10^3 ind./m² at the three sampling sites, soft-walled foraminifera reached maximum densities of 29×10^3 and 31×10^3 ind./m² at the depths of 79 m and 30 m, respectively, and accounted for 7.2% and 12.6%, respectively, of the total meiobenthos. At the third station in this area (depth 93 m), meiobenthic density was depressed and did not exceed 20 ind./m². The density of SWF was also low (8.5×10^3 ind./m²), but their proportion of the total meiobenthos was the highest (43%).

Gromiids were recorded at three stations at depths of 84-93 m near Yalta, Cape Aya and Yevpatoriya, but densities were always low (600-1600 ind./m²).

The data presented above on the contribution of protozoa to the meiobenthos along the coast of the Crimean Peninsula indicates once again that this group of benthic organisms is a permanent component of benthic communities and undoubtedly plays a significant role in the functioning of benthic ecosystems in the Black Sea.

8.2. Deep-water methane seepage area (NW of Crimea shelf, Black Sea)

Cold methane seeps are widespread in the seas and oceans (Levin, 2005). In April 1989, methane seeps were detected in the oxygen-free zone of the Black Sea during acoustic surveys on the northwestern shelf and upper slope (Polikarpov and Egorov, 1989). A decade later, data were published on methane seeps at 189 sites near the underwater Dnieper Canyon over an area 105 km long and 43 km wide, covering 1623 km² of the seafloor in the depth range 35-785 m (Egorov et al., 1998). The underwater canyon of the Dnieper Paleodelta is located in the centre of the northwestern part of the Black Sea. Later investigations of this area revealed a further 2778 seeps confined to the transition zone between the continental shelf and slope in the depth range 66 - 825 m and covering 1540 km² of the seafloor area (Naudts et al., 2006). Yanko et al., (2017a, b) described studies conducted in 2008 of methane seeps in the northwestern sector of the West Black Sea Trench that were distributed at depths of 70-905 m. Numerous seeps were found subsequently down to 2070 m depth, most of them located along the shelf edge and on the upper slope, especially on the paleo-deltas and canyons of the major Black Sea rivers: Danube, Dnepr, Dniester and Don (Egorov et al., 2003, 2011). The deepest were located in areas of faults and mud volcanoes in the central Black Sea basin (Egorov et al., 2003, Krastel et al., 2003). Thus, seepage of methane from the Black Sea floor has been recorded in three of the biogeochemical strata characteristic of the Black Sea: the oxygen zone, the transitional low-oxygen zone, and a deep water oxygen-free/sulfuric hydrogen zone.

Methane in the Black Sea is believed to originate from two sources. First, so-called fossil methane, derived from deep sedimentary reservoirs. Second, biogenic methane produced by bacterial activity (Sovga and Lubartseva, 2006). These two types of methane have a number of characteristic differences, for example, absence of homologues in biogenic methane (Lein and Ivanov, 2005).

A comparative study of the benthic community structure in areas of the Black Sea with and without methane inputs was first undertaken in 1993-1994 (Luth and Luth, 1997, 1998). Analysis of the sediments in the methane seepage areas, which differ from one another in the presence or absence of seeps, indicated that most of the biogeochemical parameters of the sediments were very similar but lower levels of organic matter and pigments were observed in the sediments where seeps were present. According to the authors, irregularities in the potential hydrolytic activity of bottom sediments in areas with gas seeps may be determined by the presence of incoming methane bubbles, which leads to a change in the sediment structure and greater habitat diversity.

Despite the reduced content of organic matter and pigments, the biomass and biological activity of bottom communities in the gas seep areas have the same values as in areas without seeps. At the same time, the predominance of larger-sized microbenthic animals where seepage is occurring is considered by the authors as an indicator of greater biocenosis stability, since the animals have a chance to live longer and reach larger sizes. In addition, methane in seepage habitats is considered an additional source of energy for zoobenthos (Luth and Luth, 1998). It is known that methane inputs to the marine environment may have an effect on benthic communities (Egorov et al., 1998; Dando and Hovland, 1992; Jensen et al., 1992; Levin, 2005]. However, some authors consider the areas in the sulfide zone with intense methane

seepage to be the most biologically productive due to the presence of anaerobic methane-oxidizing microorganisms (Lein et al., 2002; Michaelis et al., 2002).

In 1994, the distribution and structure of meiobenthos along an O₂/H₂S gradient in the same seepage areas to the southwest of the Crimean Peninsula was investigated during the 45th cruise of the R/V “Professor Vodyanitskiy” observed (77-232 m), which targeted sites where the dissolved oxygen content of the bottom water was different (Sergeeva, 2003). According to these studies, taxonomic diversity (13 major taxa) and total population density of meiobenthos in the area of gas seeps reached high values in the depth range 77-151 m, decreasing sharply at a depth of 172-232 m. SWF accounted for the greater proportion of total foraminifer densities in the depth range (78-172 m), with *Psammophaga* cf. *simplora* being the most abundant species. At a depth of 130-150 m a specific community of benthic organisms adapted to anaerobic conditions was identified and its main components included soft-walled foraminifera. The HSF fauna was represented by five species that are widespread in the Black Sea but have a low density in the study area: *Ammonia compacta* Hofker, 1964, *Eggerella scabra* Williamson, 1858 and three species of the genus *Lagena*. It is concluded that the high abundance of meiobenthos is determined by favourable trophic conditions, lack of competition from macrobenthos, a diverse range of habitat gas conditions, and adaptive capabilities of meiofauna that allow them to occupy free biotopes unfavourable for other benthic organisms.

Given these observations, it was of interest to investigate the taxonomic structure and quantitative development of meiobenthos, in particular the contribution of Protozoa to communities in the seepage area of the underwater Dnieper Canyon (SW of Crimea) along the oxygen/hydrogen sulfide gradient (Fig. 8.11). These studies were carried out within the framework of the EU HERMES project on material obtained during the R/V “Meteor” cruise in February-March 2007 (Sergeeva et al., 2012).

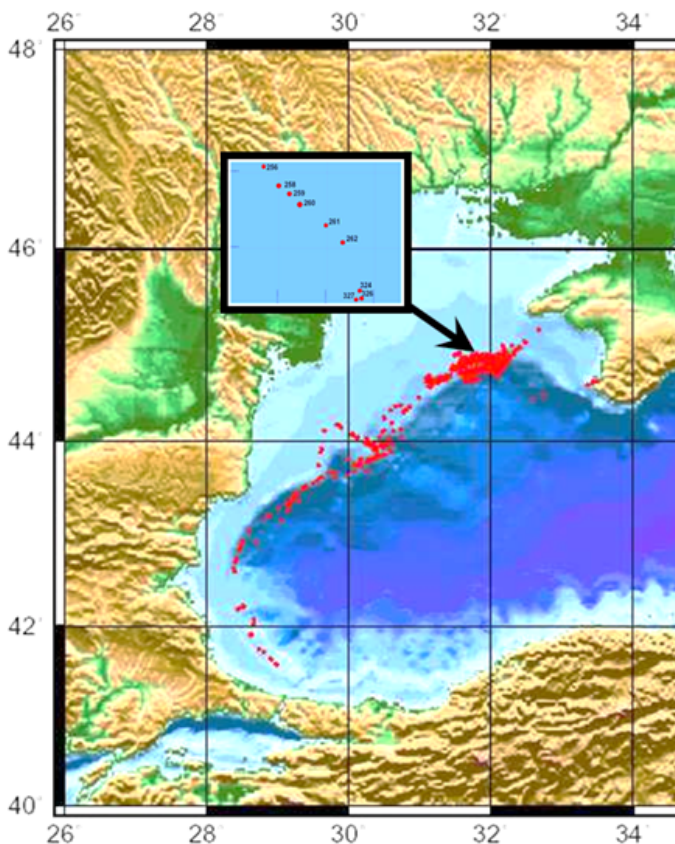


Figure 8.11. Location of sampling sites in the NW part of the Black Sea (02.07. 2007, R/V “Meteor”)

Two peaks were observed in the abundance of total meiobenthos along the depth gradient (Fig. 8.12), the larger one ($> 1500 \times 10^3$ ind./m²) at 120 m depth (normoxia), the smaller one in the "periazotic zone" at 160 m depth (815×10^3 ind./m²). Changes in SWF and HSF abundance with depth showed a similar tendency. Hard-shelled forms peaked at a depth of 160 m (48×10^3 ind./m²) and were not detected below 170 m. Soft-walled forms peaked at a depth of 170 m (54×10^3 ind./m²) and were distributed in small numbers down to 240 m. The density of both groups decreased sharply after these peaks (Sergeeva et al., 2012).

The abundance and bathymetric distribution of gromiids in the area studied were distinctive. Under normoxic conditions (depth 120-130 m), their density significantly exceeded that of both groups of foraminifers. In conditions of extreme hypoxia (depth 140-170 m), gromiids were not abundant (densities from 300 to 1400 ind./m²) and they maintained low numbers (200-800 ind./m²) also in the zone of anoxia with hydrogen sulfide (to depth 240 m). However, an unexpectedly sharp spike in their abundance (greater than 30×10^3 ind./m²) was recorded at one of the two stations sampled at 210 m depth. At this depth, gromiids and nematodes were the only

components of the benthic communities. Obviously, this unevenness in the development of protozoa in the study area may be related to the heterogeneity of the environment caused by methane seepage.

The proportion of HSF as part of the total meiobenthos abundance was 0.3-6%, and in conditions of oxygen depletion (150-170 m depth) they accounted for 3.7-6%. SWF contributed 0.6-28% of the total meiobenthos, the maximum value being in the oxygen-free zone associated with hydrogen sulfide at a depth of 170 m.

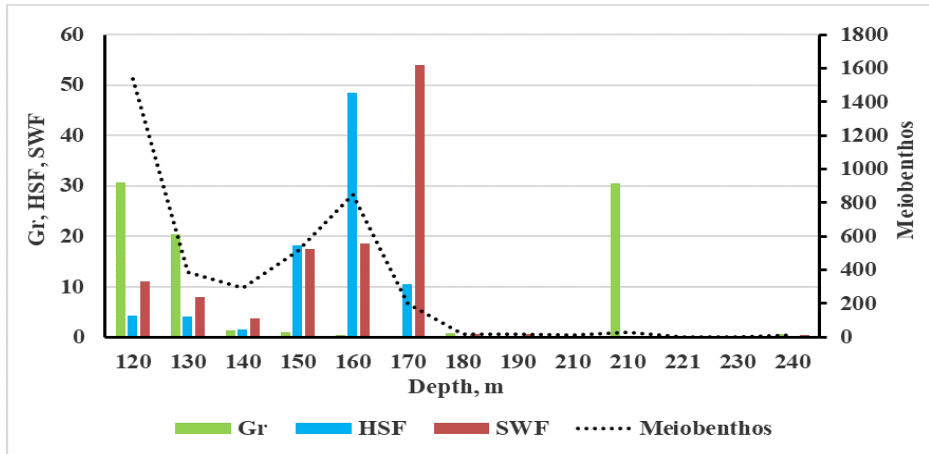


Figure 8.12. Density ($N \times 10^3 \text{ ind./m}^2$) of protozoans and meiobenthos as the whole along the normoxic to hypoxic and anoxic zone in methane seeps area of the Dnieper Canyon (R/V “Meteor”, 02.03.2007)

The contribution of gromiids to the total meiobenthos under normoxic conditions (120, 130 m) was 2-5.3%. In the anoxic/sulphidic zone (180-240 m) gromiids were virtually absent except at 210 m, where they made up 90% of the total meiobenthos.

The area of methane seeps in the western Black Sea is attracting increasing attention from researchers. In September 2008, a study of meiobenthos was conducted to identify the possibility of using it as an indicator of accumulations of hydrocarbon gases, primarily methane, in the Black Sea (Yanko et al., 2017b). Based on a combined analysis of abiotic (physico-chemical parameters of the water column, geochemical, lithological, mineralogical properties of bottom sediments) and biotic (quantitative and taxonomic composition of foraminifers, nematodes, ostracods), the authors recommended using meiobenthic attributes as a search tool for methane accumulations.

Studies were carried out in the central part of the northwestern sector of the West Black Sea trough in the depth range of 70-905 m. Four zones were distinguished within the water column: normoxic ($>2 \text{ mg/L}$), hypoxic ($<2 \text{ mg/L}$), anoxic (0 mg/L), and sulfidic (0 mg/L oxygen and free sulfide present). During the study period, the first zone, according to the Yanko et al. (2017a, b), only included the upper 80 m of the water column. The content and saturation of water with oxygen decreased from 8.6 mg/L (103.4%) in the surface water layer to 0.46 mg/L (4.9%) at 180 m. A sharp decrease occurred at a depth of 80 m. This does not correspond to our data (Sergeeva

et al., 2014), according to which the decrease is located at 120 m. Yanko et al. (2017a) suggest that this difference reflects an unstable position of the boundary, apparently related to local conditions, seasonal variability, etc. The authors note that in the area they studied, meiobenthos in general, and its main constituent groups, were characterised by low abundance and low species numbers compared with other areas of the Black Sea. The foraminifera and nematodes each accounted for 33% of all meiobenthos, while foraminiferal dominance was recorded in the east. The maximum density of all meiobenthos was 33×10^3 ind./m². Its average density to the east of the Odessa-West Crimean Fault was higher than to the west, 1560 and 950 ind./m², respectively.

8.3. Bays of Sevastopol

The contribution of soft-walled and hard-shelled foraminiferans and gromiids to Black Sea meiobenthic communities in the region around the Crimea was considered based on two examples, namely the Kruglaya (Omega) and the Sevastopol bays within the city of Sevastopol. The choice of these bays reflects the different nature and level of anthropogenic impact on these semi-enclosed ecosystems. There are quite a lot of publications on the structure of meiobenthic communities in the different bays of Sevastopol and the response of meiofauna to environmental factors, so here we only provide information on the distribution of Gr, SWF and HSF and their quantitative importance as part of the total meiobenthic communities.

The distribution of foraminifera was studied using data obtained during a meiobenthos survey as part of the international project "PERSEUS" (2013).

8.3.1. Kruglaya (Omega) Bay

Kruglaya (Omega) Bay is a shallow water area up to 1 km wide in the middle part. Depths reach 5 m in the central part of the bay and 10 m at the boundary with the open sea. The bottom is sandy silt with a small amount of broken shell material. Water exchange with the open sea is limited, except for winter storm surges to the north and north-west. For this reason, the waters of the Bay are well aerated during the cold season due to hydrodynamics and vertical convective mixing.

During the warm season the Bay is characterized by vertical stratification due to a seasonal thermocline, which leads to the development of a two-layered water column and poor ventilation of the bottom layer at relatively high temperatures. This contributes to intensive oxygen consumption by various biological and chemical processes. There are no sources of industrial pollution in the Bay, but the discharge of domestic wastewater and the intensive generation of organic matter during the warm period of the year lead to a pronounced deficit of O₂ at the surface and in the bottom sediments. Although the bay is located inside the city, there are no industrial facilities on its shores, only recreational spaces, parks and leisure centres. One would expect the bay to have natural conditions, but this is not the case. Limited water exchange with the open sea, sustained vertical water stratification, domestic and stormwater discharges have resulted in anoxia in bottom sediments (Zaika et al., 2011).

Meiobenthos studies were undertaken at eight stations in the depth range 3-16 m (Fig. 8.13). Meiobenthic densities in the Bay are quite high ($>134 \times 10^3$ to 550×10^3 ind./m²). Minimal numbers were recorded at 3 m depth in the centre of the bay, with maximum values recorded at depths of 5 and 8 m in the eastern part at two adjacent

stations (7 and 27). HSF were recorded in low numbers (300-1100 ind./m²) at five stations only (Fig. 8.14).

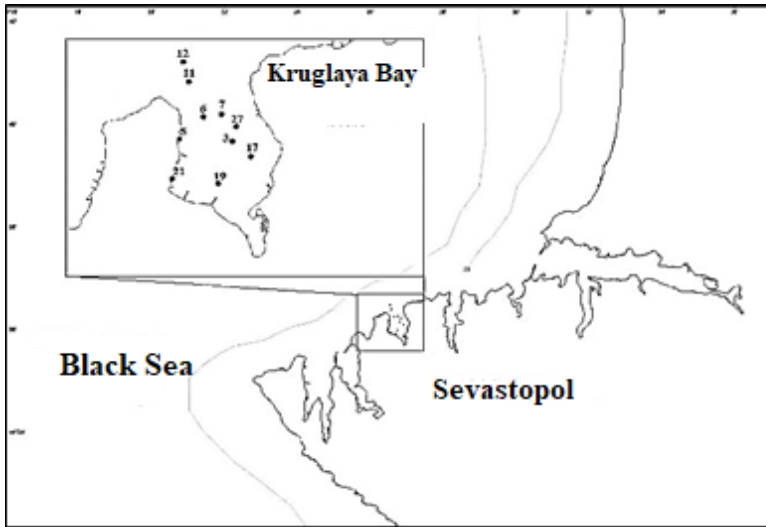


Figure 8.13. Scheme of meiobenthic stations in Kruglaya Bay (October, 2013)

No great changes were found in the quantitative development of soft-walled foraminifera within the Bay during this period of study. The rather monotonous pattern was interrupted only at station 3, where SWF were most abundant. The densities of SWF ranged from 2210 to 6100 ind./m² and their contribution to the meiobenthos ranged from 0.5 to 1.7%.

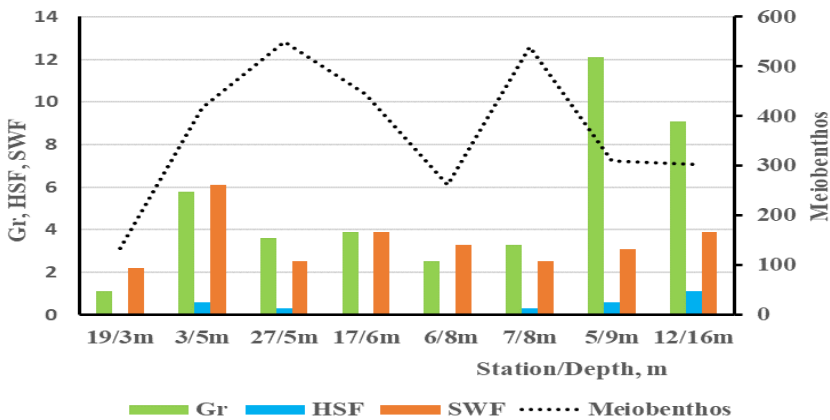


Figure 8.14. Density (N x 10³ ind./m²) of protozoans and meiobenthos on the whole in Kruglaya bay (October, 2013)

During a study of seasonal changes in species composition and quantitative development of the SWF at one of the stations in Kruglaya Bay in 2010, 11

representatives of this group were identified (Sergeeva and Anikeeva, 2014). The most frequent were four species, *Vellaria pellucida*, *V. sacculus*, *Bellarium rotundum*, *Krymia fusiformis*, and three morphotypes, *Bathyallogromia* sp.1, *Psammophaga* sp. and *Psammospheridae* sp. *Vellaria pellucida* was recorded in all seasons, but *V. sacculus* was the most abundant overall (300×10^3 ind./m²). Throughout the year 1-3 species of allogromiids were usually found, but in May and September the number of species increased to 5-6. The average density of soft-walled foraminifera in Kruglaya Bay during the year was 24×10^3 ind./m² and their development peaked in May (about 400×10^3 ind./m²). The largest contributions to this peak were made by *V. pellucida*, *V. sacculus* and *B. rotundum*.

8.3.2. Sevastopol Bay

Sevastopol Bay is the longest in the south-western part of Crimea, extending 7.5 km inland, with a width of up to 1 km near the open sea. The depths range from 22 m at the head of the Bay to 3 m in the inner part, with the average depth being 12.5 m. The bottom sediments of Sevastopol Bay are represented by dark-grey and black pelitic silt at depths of 5-18 m. Near the Bay mouth at a depth of 17-19 m, these silts are replaced by silty sands and gravels with admixture of stones, while along the shores at a depth down to 1 m between rock outcrops there are sands and coarse-clastic sediments with a typical particle size of 1-2 mm but also presence of large particles over 7 mm in diameter.

The inner part of the Bay is affected by hypoxia as a result of industrial pollution in recent decades, which has limited water exchange and freshwater inflow. The biogeochemical conditions of the sediments in the Bay environment are so extreme that hypoxia has become a regular feature of the interior in summertime. In addition, sulfidic sediments serve as a source of hydrogen sulfide for the lower water layer, influencing the living benthic communities. Nutrients are released into the Bay via the waters of the Black River; they are also brought in by urban and industrial wastewater, resulting in intense eutrophication of the Bay's waters.

As a result of these factors, sediments in Sevastopol Bay are rich in organic carbon, which averages 4% but may locally be as high as 7%. Oxygen uptake is extensive, both in the sediment and in the immediately overlying water, contributing to anoxic and hypoxic conditions in the area (Orekhova and Konovalov, 2009a, b). Examples of the complete disappearance of oxygen in the bottom layer of water and the emergence of hydrogen sulfide at a concentration of $0.8 \text{ ml} \times \text{L}^{-1}$ were recorded in some parts (Zaika et al., 2011).

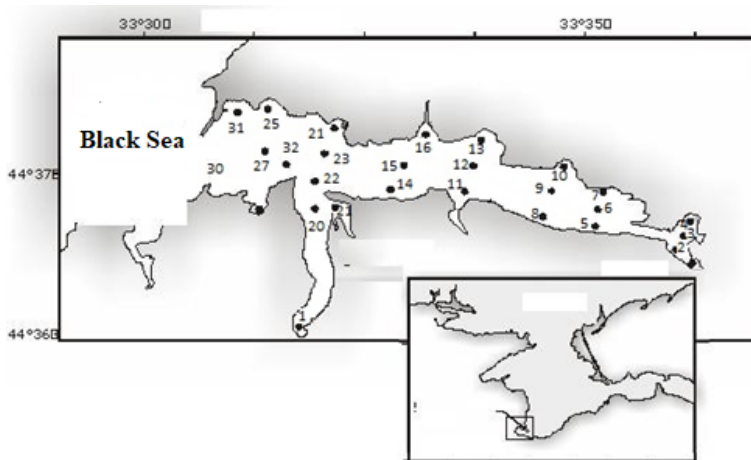


Figure 8.15. Meiobenthic stations conducted in Sevastopol Bay (June, 2013)

Meiobenthos of Sevastopol Bay was studied in June 2013 at 18 stations located on several transects along the Bay from the inner part to the sea outlet (Fig. 8.15). The bottom sediments at these sampling localities were black silt of varying consistencies with a perceptible smell of hydrogen sulfide. At most stations there was an oil film on the surface of the sediments.

Despite strong pressure from a wide range of natural and, more importantly, technogenic factors, the quantitative development of meiobenthos was high, albeit with some exceptions at individual stations (Fig. 8.16). The maximum density ($610 \times 10^3 \text{ ind./m}^2$) was recorded at the outlet of the Bay into the sea, the minimum ($14 \times 10^3 \text{ ind./m}^2$) at its inner extremity. The distribution of meiobenthos was uneven along the Bay, but there was a tendency for its abundance to increase towards the open sea.

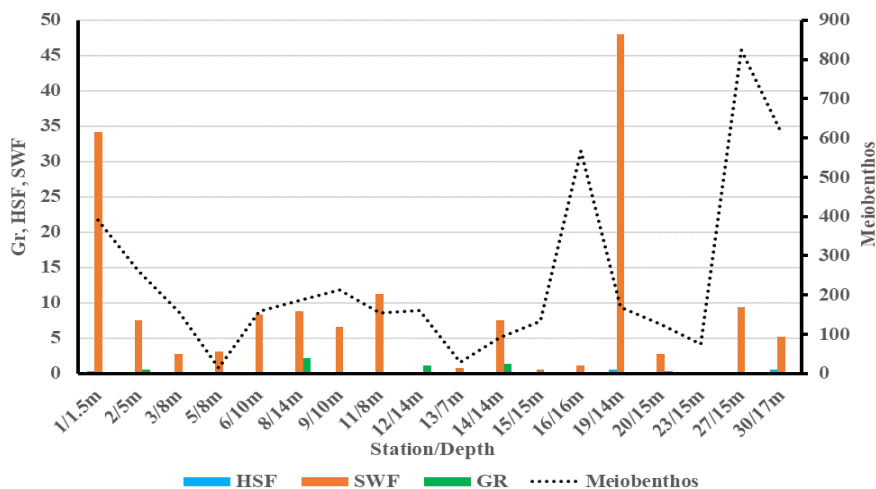


Figure 8.16. Density ($N \times 10^3 \text{ ind./m}^2$) of protozoans and meiobenthos on the whole in Sevastopol Bay (June, 2013)

Soft-walled foraminifera were found at 16 of the 18 stations investigated, while hard-shelled forms were found at only three of them, with a maximum density 1380 ind./m² and minimum density 550 ind./m². The SWF density varied from 5.5 x 10³ to 48 x 10³ ind./m². The proportion of soft-walled foraminifera as part of the meiobenthos was minimal (0.2% to 0.4%) in the middle part of the Bay (st. 15 and 16), rising to 1.1-8.8% at the remaining stations, except for st. 5 and 19, where they accounted for 22 - 28.5%.

An earlier study (2002) of the seasonal dynamics of density and species composition of SWF taxa at three sites in Sevastopol Bay (Sergeeva and Anikeeva, 2018) showed that SWF diversity is low under extreme conditions (permanent presence of hydrogen sulfide in bottom sediments). During the year only 8 morphotypes were recognised, 4 of them identified to species level, the rest to genus. *Psammophaga* sp. (*Psammophaga* cf. *simplora*) remained the dominant species during each month, accounting on average for about 75% of the total SWF. Another common species, *Vellaria pellucida*, averaged 12.4% of the total SWF. The other species of soft-walled foraminifera were observed sporadically, represented by only single specimens. Hard-shelled foraminifera and gromiids were almost absent in the habitat-unfriendly polluted bottom sediments of Sevastopol Bay.

Our studies of these two contrasting Bays have shown that the density of soft-walled foraminifera in Sevastopol Bay is quite variable, in contrast to the more even distribution in Kruglaya Bay. Although the average SWF density values are broadly similar (8.7 x 10³ ind./m² for Sevastopol Bay and 3.4 x 10³ ind./m² for Kruglaya Bay), a distinctive feature of the SWF distribution in Sevastopol Bay is the increased abundance at two stations (St. 1 and St. 19) and the higher density at other stations, in comparison with Kruglaya Bay. Correspondingly, the maximum contribution of soft-walled foraminifera to meiobenthic communities in these two areas is also different: 1.6% in Kruglaya Bay and 28.5% in Sevastopol Bay. At present we are not able to provide an explanation for this difference.

Given the high levels of pollution in Sevastopol Bay, one would expect a minimal development of SWF and meiobenthos in general. However, our data leads to the conclusion that of the protozoan groups considered, SWF are the most tolerant to these extreme habitat conditions, and in particular to oil pollution and the presence of hydrogen sulfide.

8.3.3. Anthropogenic underground channel in Balaklava Bay

The first observations of benthic protozoans in an underwater channel built in 1950s (Fortifications “Balaklava”, Sevastopol) were made in 2020. Over 400 thousand cubic meters of rock were removed during construction. The thickness of concrete wall facing of the underground complex is 110 cm on average. The channel is located in Balaklava Bay extends into Tavros Mountain (44°30'1.8"N, 33°35'48.48"E), with an entrance close to the apex of the Bay (Fig.8.17).

The total length of the channel is 608 meters, its central and southern sections are 12 meters wide and its northern section is 22 meters wide. The volume of water is 76 thousand m³. There is natural illumination of the water surface only in the entrance and exit areas, but the channel has artificial illumination along most of its main length. At the time that samples were collected, the water temperature within the channel was

10°C, the salinity varied from 18.9 to 19.2‰, the pH was 7.1–7.5, and the redox potential varied from -256.4 to -95.3.

A description of this artificial underground water body and its macro- and meiobenthic inhabitants is presented in the work of Sergeeva et al. (2021). Four sites (stations) were selected to study the benthos: stations 4 and 1, located at the entrance and exit of the channel, respectively; stations 3 and 2, located in the central least illuminated part (Fig. 8.17, C, D). Station 1 is 50 m from the channel exit, station 2 is 150–200 m from the channel exit, station 3 is in the centre of the channel. The channel entrance (station 4) faces north-east. Accordingly, the illumination from sunlight is different on the north-western and south-eastern channel walls.

Fouling of the channel walls and the fauna of its bottom sediments were studied. At each station, two replicate bottom sediments samples ($S=0.04 \text{ m}^2$) for macrozoobenthos were collected by a diver, while for meiobenthos samples were taken using three replicate meiobenthos tubes ($S=18 \text{ cm}^2$) in three replicates. Fouling of the channel walls (macro- and meiobenthos) was investigated at 1.5 m depth using standard hydrobiological frames ($S=0.04 \text{ m}^2$) with a silk cloth bag with a mesh diameter of $64 \mu\text{m}$ (two replicates).

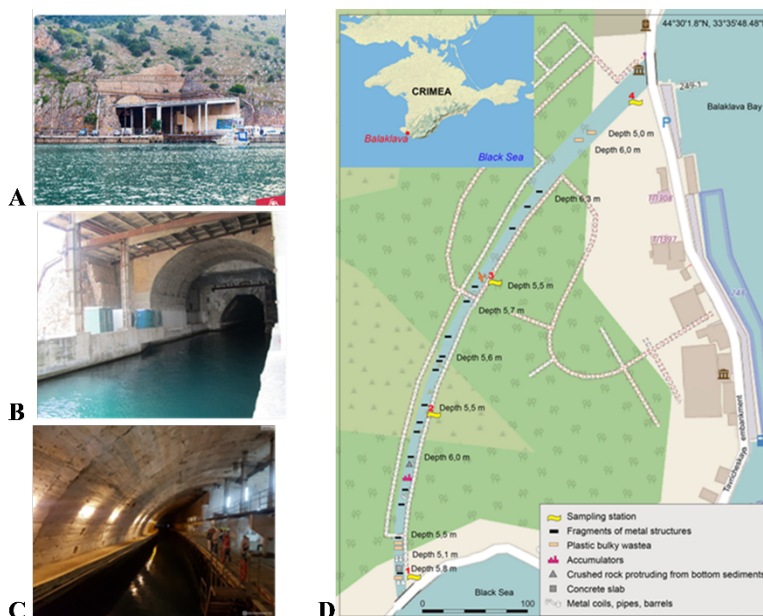


Figure 8.17. Museum of Military History of Fortifications "Balaklava" in Mount Tavros: A – entrance to the Museum from the side of the Balaklava Bay embankment (photo by A. Zatsepin); B – northern entrance part of the channel from the side of the embankment of the Bay; C – internal view of the channel with artificial illumination in central parts; D – topography of antropogenic objects in the underground channel and the benthos sampling points

Water depths at the time of the survey were from 5.0 to 6.3 meters, with an average depth of 5.5 meters. At the bottom there is a layer of silt more than 0.5 m

deep. The silt is dark gray and black in color with a smell of hydrogen sulfide. There is no doubt that sediment accumulation processes in the channel are very active and uneven due to allochthonous suspended matter brought through the entrance and exit, and the dynamics of water exchange associated with conditions in the adjacent bay area. The bottom of the channel was littered with plastic trash – cases, boxes, chairs, fishing nets and *Mytilaster lineatus* halyards, car tyres etc. The walls of the channel are covered with biofouling from Bivalvia, Bryozoa, Porifera and Ascidiacea.

Fouling of the channel walls and the fauna of the bottom sediments were studied, revealing that fully-fledged macro- and meiobenthos communities are present. The meiobenthos in the sediment was represented by 15 taxa of Protozoa and Metazoa of high rank with variation of their development (6–12 taxa) at different stations. Meiobenthic biofouling communities included 18 faunal groups of similar rank (type, class, order) with little difference in the number (11–14 taxa) at each station. The average density of meiobenthic communities in the channel sediments was 2.8 times higher than in biofouling communities.

Analysis of the samples revealed more detailed information about the benthic protozoans (Gr, SWF and HSF) in the biofouling communities of the channel wall (depth 1.5 m) and of bottom sediments. It should be noted that free-living Ciliophora were not observed, but epibiotic ciliates (peritrich ciliate and suctorian) were found on representatives of some meiofauna groups (Halacaridae, Nematoda, Oligochaeta, Harpacticoida) (Sergeeva et al., 2021).

SWFs live in bottom sediments throughout the channel, with their maximum abundance (3500 ind./m²) recorded in the middle part. The distribution of gromiids showed a different trend: the highest population density (nearly 3000 ind./m²) was confined to the more illuminated station (point 1) near the entrance to the channel. HSF are recorded in small numbers only at stations 2 and 4 (Fig. 8.18).

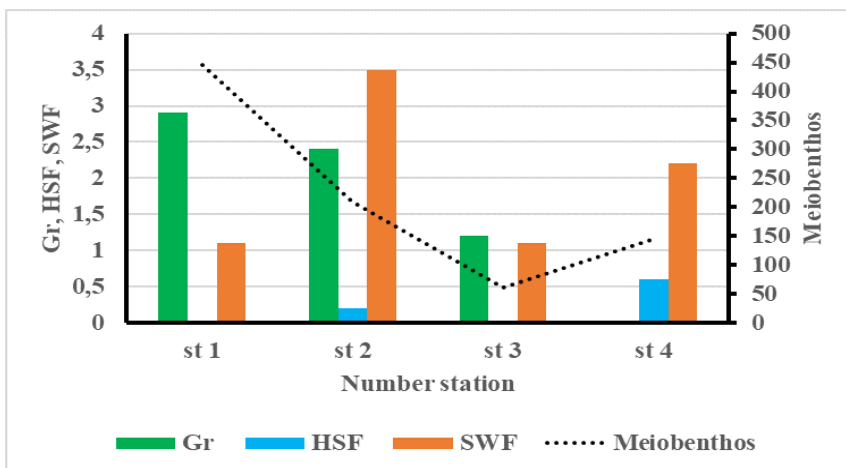


Figure 8.18. Change in abundance (N x 10³ ind./m²) of protozoans and total meiobenthos in bottom sediments of the underground channel (Balaklava Bay, 03.2020)

Preliminary examination of the samples revealed the distribution of protozoans on the channel walls differed sharply from that in the bottom sediments (as shown in Figs. 8.18, 8.19). Gromiids were present in both habitats and were represented by three morphotypes.

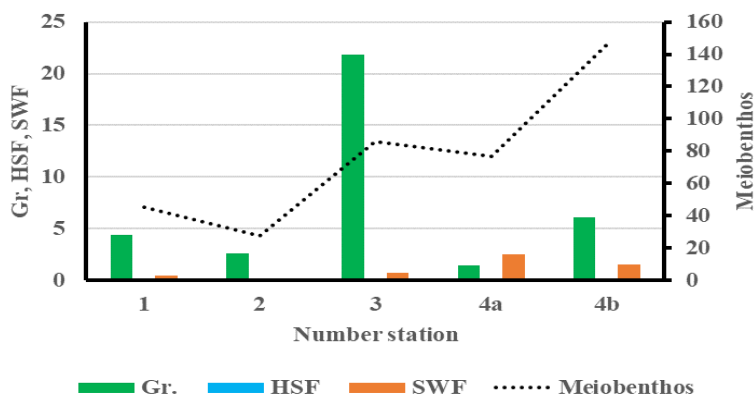


Figure 8.19. Change in abundance ($N \times 10^3 \text{ ind./m}^2$) of protozoans and meiobenthos on the whole in the fouling of the walls in the Underground channel (Balaklava Bay, 03.2020)

The ecosystem of Balaklava underground channel is a unique structure that can be considered as an anthropogenic analogue of a Black Sea cave. Undoubtedly, the formation of bottom communities and the biofouling on the channel walls are determined by a set of abiotic and anthropogenic factors within of this artificially created environment. Abiotic factors include the climate in the surrounding area (Balaklava Bay), the microclimate of the underground space, and the hydrodynamic properties of the water within and adjacent to the channel. Anthropogenic factors include artificial material (concrete, metal, plastic and other materials), waste water discharge, etc. The biofouling of the walls was most developed in these entrance parts. The quantitative development and distribution of the protozoan components of the meiobenthos are undoubtedly determined by the structure of inhabitat here macro- and meiobenthos, the heterogeneous nature of the fouling, and anthropogenic pollution of bottom sediments. During the years that the channel has existed, a specific taxocenosis of protozoans has formed within it, which plays a special role in this ecosystem.

8.3.4. Seasonal dynamics of the foraminifera and gromiida density under normoxia/hypoxia conditions in the shallow areas of the Crimea

In addition to the permanent anoxia of the huge volumes of deep waters in the Black Sea, seasonal oxygen deficiency in the near-bottom waters may also occur in shallow coastal areas. For example, bottom-water hypoxia is observed in the bays near Sevastopol, where the degree of oxygen deficiency varies on a seasonal basis (Kondratiev, 2010; Svishchev et al., 2011). The study of seasonal successions in bottom sediments revealed that the vertical distribution of oxygen in the water mass and the

upper limit of occurrence of sulfides in the bottom sediments in Sevastopol region is also variable (Orekhova and Konovalov, 2009a, b).

In an interdisciplinary chemical and biological study, Zaika et al. (2011) showed that, depending on the season and the place of observation, the upper boundary for the presence of sulfides within the sediment can occur varied from the bottom surface to a depth of >60 mm. These data, which were taken as a proxy for the degree of hypoxia and depth appearance of hydrogen sulfide, were compared to the number of macrobenthic organisms. This study showed that the total number of macrobenthos decreases as hydrogen sulfide approaches the surface of the sediment, and the response of different taxonomic groups is not identical (Zaika et al., 2011). Although benthic animals have different responses to hypoxia at the species level, when comparing size groups, the meiofauna is generally less sensitive to hypoxia than macrofauna (Austen and Wibdom, 1991; Moodley et al., 1997; Levin et al., 2009).

Studies of the distribution and seasonal changes in the taxonomic composition of the macrobenthos and meiobenthos have revealed specific responses by certain benthic taxa to contrasting hypoxic environments at three locations in the bays near Sevastopol. Some taxa showed a decrease in their total density as the hydrogen sulfide rises up to sediment surface. In contrast to this pattern, the densities of some nematode species increased in response to this phenomenon (Zaika et al., 2011).

Here, we compare seasonal changes in the abundance of benthic protozoans (soft-walled and hard-shelled foraminifera, and gramiids) in three shallow-water coastal areas near Sevastopol under different hypoxic conditions. Bottom sediments were sampled for meiobenthos every 45 days during July 2009 to May 2010 by divers using a tube sampler. Two or three replicates, each covering an area of 18.1 cm² to a depth of 5 cm, were obtained. At the same time, oxygen, sulfides, oxidized and reduced forms of iron, reduced forms of manganese and iron sulfide were determined in the sediment pore waters at the three sites near Sevastopol (Orekhova and Konovalov, 2009a, b).

The boundary at which hydrogen sulfide (H₂S) appeared in the sediments changed from the sediment surface to 60 mm depth, depending on the site and the season (Zaika et al., 2011). The three sampling areas ('micropolygons') in the vicinity of Sevastopol differ in the nature and degree of anthropogenic pressure (Fig. 8.20). The first area (1) is located in Kruglaya (Omega) Bay. The second (2), termed the outer harbor, is located in Sevastopol coastal waters and serves as a control point. The third (3) is located in Sevastopol Bay at the entrance to the Yuzhnaya Bay. Detailed ecological characteristics of these study areas were given in the work on macrobenthos (Zaika et al., 2011; see this paper 8.3). The water depths are 8-10 m in Kruglaya Bay, 18-21 m in the outer harbor, and 11-16 m in Sevastopol Bay. We summarise seasonal changes of the abundance of benthic protozoans as part of the meiobenthos in these three contrasting areas.

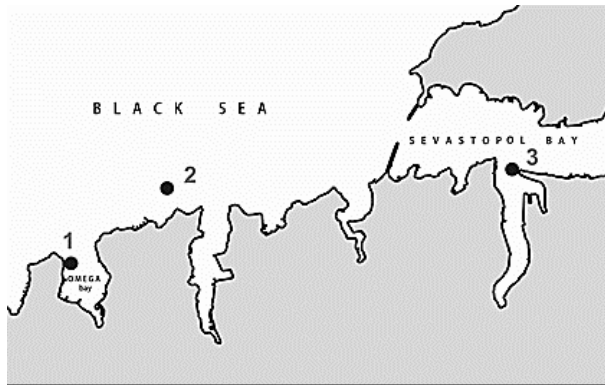


Figure 8.20. Sampling points in the Sevastopol bays. 1- Kruglaya (Omega) Bay, 2 – “outer harbor”, 3- Sevastopol Bay (at one input in the Yuzhnaya Bay).

Different habitat conditions in these areas determine the pattern over time in the development of both the meiobenthos as a whole and its constituent components. This can be clearly seen in the figures showing the seasonal dynamics of meiobenthos and protozoans.

In the more environmentally friendly regions of Kruglaya Bay and “outer harbor”, different benthic protozoan groups display different patterns of quantitative development (Fig. 8.21). At the first site (Kruglaya Bay, 10 m depth) we found only SWF and Gr. The SWF were extremely abundant in May 2010 ($476.8 \times 10^3 \text{ ind./m}^2$), accounting for almost 50% of the density of the meiobenthos as a whole. In other months they were relatively uncommon. Gromiids were most abundant in March and May 2010 ($97.7\text{--}153.8 \times 10^3 \text{ ind./m}^2$), and in March they accounted for almost half of the meiobenthos. HSF were not detected in any of the samples from this site in 2009 and 2010.

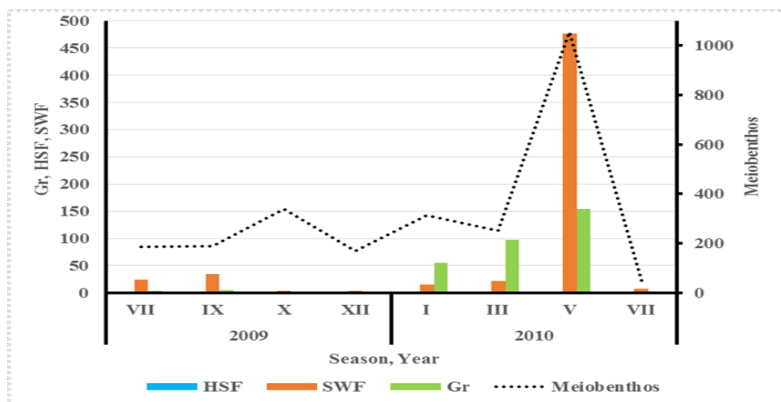


Figure 8.21. Dynamic of density ($N \times 10^3 \text{ ind./m}^2$) of protozoans and total meiobenthos at site 1 in Kruglaya Bay

At the control site (site 2, “outer harbor”), all three groups of benthic protozoa were present, but density of each group did not exceed several tens of thousands of

ind./m² (Fig. 8.22). Gromiids and SWF were seen throughout the observation period with gromiids usually being dominant. HSF were found only during three of the eight months, but they reached a significant abundance (48 x 10³ ind./m²) during July 2009 (Fig. 8.22).

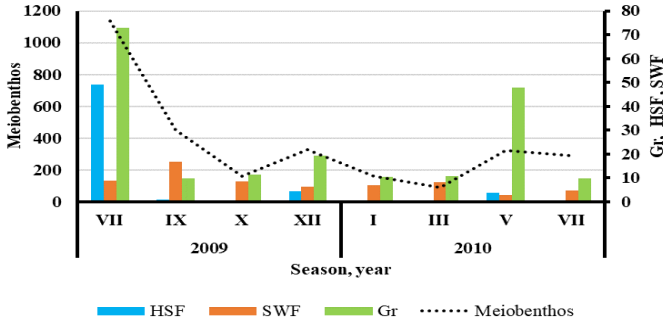


Figure 8.22. Dynamic of density ($N \times 10^3$ ind./m²) of protozoans and meiobenthos as a whole at control site (Sevastopol Bay, 2009, 2010).

The situation was completely different in Yuzhnaya Bay, which is the most environmentally stressed site with high level of pollution by oil products and hydrogen sulfide (Fig. 8.23). All three benthic protozoan's groups were present but their abundance is different. SWF and Gr were a constant component of the meiobenthos, but HSF were found only in three samples and in small numbers.

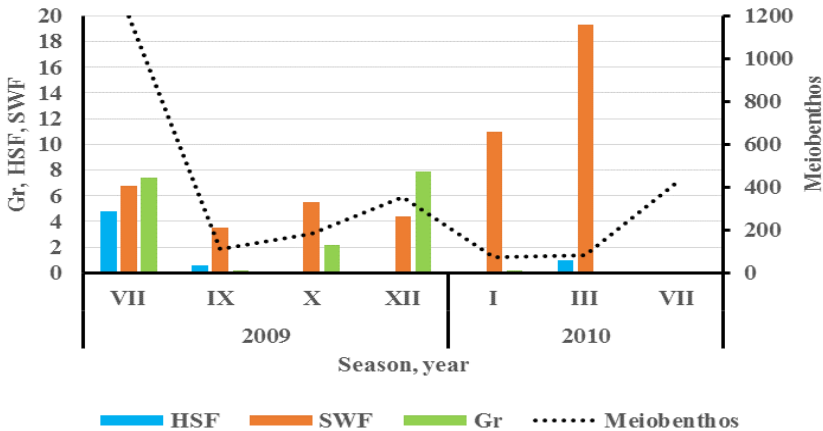


Figure 8.23. Dynamic of density ($N \times 10^3$ ind./m²) of protozoans and meiobenthos on the whole in Yuzhnaya Bay.

The data summarized above suggests the following conclusion. Bottom protozoans are a constant component of meiobenthic communities in different areas of the Sevastopol region that experience different degrees of anthropogenic pressure. Undoubtedly, their distribution and quantitative development is determined not only by seasonal temperature changes, but also by the structure of the biotopes and the

nature of anthropogenic impact. The study of benthic protozoans as part of benthic communities is necessary because they play a huge role in the cycle of organic matter in benthic ecosystems.

CHAPTER 9

BENTHIC PROTOZOANS AS A COMPONENT OF BOTTOM COMMUNITIES AT THE SEA OF AZOV

The Sea of Azov is a relatively small body of water, connected to the Black Sea from the north-east by the Kerch Strait. It is 343 km long, 231 km wide and mostly ranges from 6.8 to 8 m in depth with a maximum depth of 13 m. The surface water temperature in summer is around 24 - 26 °C. Because of its shallow depth, the sea warms up quickly in summer and freezes either completely or partially in winter. The salinity is quite low, varying from 1‰ to 11.5‰, reaching a maximum value in the area of the Kerch Strait. The main negative anthropogenic impacts are related to the discharge of untreated domestic and industrial sewage into the sea. Pollution by oil products arising from cargo traffic and port activities has become catastrophic. Dissolved oxygen depletion in the bottom waters of the Sea of Azov is a common phenomenon in summer. This is caused by the presence of a large amount of organic matter in the water column and bottom sediments, the oxidative biodegradation of which causes oxygen consumption in the bottom layers to exceed its input, especially under stagnant water conditions.

The inter-seasonal fluctuations in the quantitative development of meiobenthos in the south-western waters of the Sea of Azov subject to multiple sources of pollution has been studied using data obtained from several cruises of the R/V Professor Vodyanitsky in 2016 and 2017. Monitoring data on seasonal changes in meiobenthos abundance and composition within a polygon (Fig. 9.1) covering depths of 6-11 m (4 stations) of the north-east Crimean coast of the Sea of Azov will be discussed in a separate article. Here we report for the first time the abundance and distribution of soft-walled and hard-shelled foraminifera within the boundaries of this polygon and estimate their contribution to meiobenthos communities on a seasonal basis.

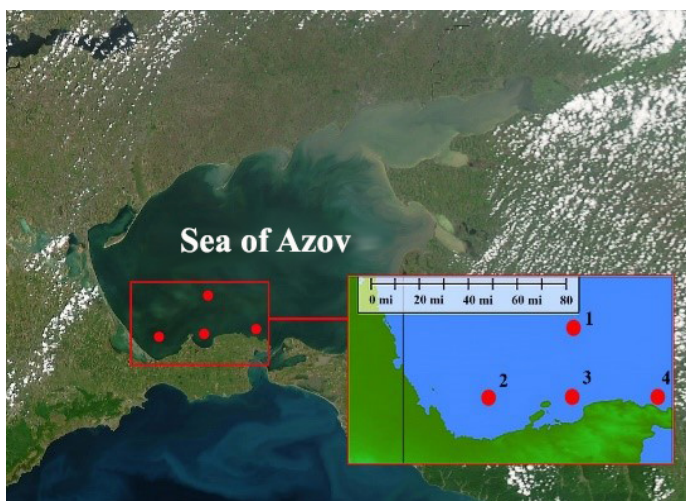


Figure 9.1. Scheme of meiobenthic stations in the south-western part of the Sea of Azov (2016-2017)

The sediments at all the stations consisted of silt (with varying degrees of admixture of shell rock). In winter the sediments had a pungent hydrogen sulfide smell.

The data obtained allow us for the first time to illustrate changes in the quantitative development of meiobenthos in the Sea of Azov, and to assess the contribution of its protozoan components, Gr, HSF and SWF, to meiobenthic communities over a seasonal cycle (Fig. 10.2). The density of meiobenthos assemblages in the polygon at different times of the year varied considerably between sites. The lowest value (1.7×10^3 ind./m²) was recorded at station 1, located to the north of the Crimean coastal zone, while the highest values (537×10^3 ind./m²) were recorded at station 4. Of the benthic protozoan taxa considered, only soft-walled foraminifera were observed in the investigated polygon during all periods studied. At the same time, their density varied widely, from 0.6×10^3 to 26.7×10^3 ind./m². Despite the fact that SWF densities at the stations are low, their contribution to meiobenthos is nevertheless very significant. Thus, at Station 1, the meiobenthic density was $1.7\text{--}35.4 \times 10^3$ ind./m² and for SWF it ranged from 400 ind./m² in December to a maximum of 26.7×10^3 ind./m² in July. However, the contribution of this group of protozoans to the total meiobenthic abundance was 4.7% (December), 33.3% (February), 12.5-15.8% (April and October) and 75.5% in July.

To the west (St. 2), meiobenthic densities were generally similar in October and July (about 60×10^3 ind./m²), reaching values of 116×10^3 ind./m² and 155.5×10^3 ind./m² in February and December, respectively. The density of SWF did not exceed 0.8×10^3 - 1.7×10^3 ind./m² in all months of study, but in December it reached 14×10^3 ind./m². The contribution of SWF to the quantitative development of the meiobenthos ranged from 1.2 to 9%.

Meiobenthic densities were higher towards the east (St. 3). They were lowest (38.7×10^3 ind./m²) in February, increasing markedly ($70.1\text{--}100.3 \times 10^3$ ind./m²) in December, July, and reached maximum values ($263\text{--}264 \times 10^3$ ind./m²) in April and October. The densities of SWF were relatively consistent ($1.1\text{--}1.7 \times 10^3$ ind./m²) from February to October, increasing slightly by April and July ($6.1\text{--}6.3 \times 10^3$ ind./m²) and reaching a maximum in December (26.2×10^3 ind./m²). The contribution of SWF to the total meiobenthic density during the periods studied was not high (0.6-2.9%), but in December they accounted for 37% of the total meiobenthos abundance.

Meiobenthic density was highest (generally $173 \times 10^3\text{--}537.1 \times 10^3$ ind./m²) near the Kerch Strait (station 4), although with a lower value (67×10^3 ind./m²) recorded in February. SWF were found in small numbers in October and December (not more than 200-600 ind./m²), but during the other survey periods their abundance at this station was higher ($5.5 \times 10^3\text{--}7 \times 10^3$ ind./m²). The proportion of this group of foraminifera among the meiobenthos in the Kerch area was low (0.1-3.7%).

HSF were found only in October at stations 2 and 3. Their numbers ranged from 400 to 2200 ind./m². Gromiids were also not very common (Fig. 9.2). In February and October, they were recorded only at stations 4 and 3, respectively, in equal densities (1700 ind./m²). In the summer months, they were found at three stations, but in minimal abundances (200-800 ind./m²).

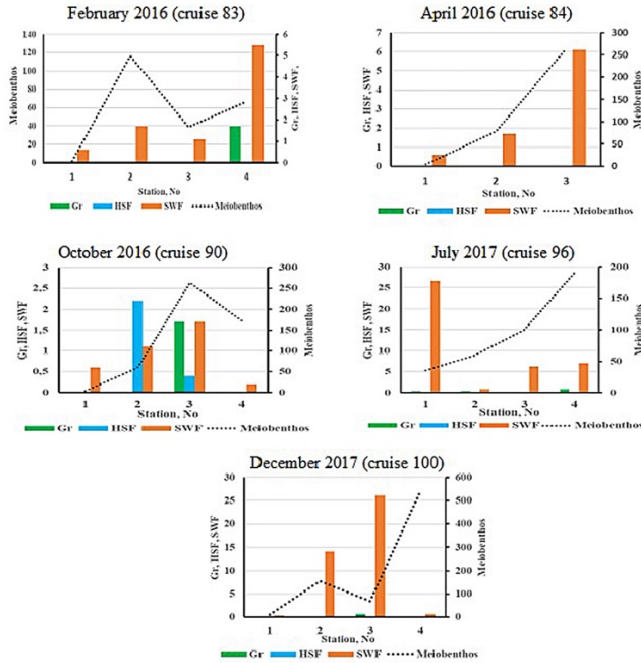


Figure 9.2. Population density ($N \times 10^3 \text{ ind./m}^2$) trends of Meiobenthos on the whole, SWF, HSF and Gr in the southwestern coastal zone of the Sea of Azov in different seasons (2016-2017, R/V “Professor Vodyanitsky”)

The results presented above suggest that soft-walled foraminifers are a permanent component of the bottom communities of the western waters of the Sea of Azov. The limited material available to us does not permit generalizations about the spatial distribution of Gr, SWF and HSF. However, these groups undoubtedly inhabit large areas of the Sea of Azov, including the Sivash Bay, and make a substantial quantitative contribution to the bottom communities.

Some common species of soft-walled foraminifera are widely distributed in the Sea of Azov, as well as in the Black Sea and under extreme conditions (hypoxia/anoxia, hypersalinity) (see Chapters 3,4). SWF, in particular *Psammophaga* cf. *simplora*, were first recorded in meiobenthic collections from the Sea of Azov in 2001 (Sergeeva N.G., unpublished data). Although not numerous, they were found at 8 stations and in different salinity conditions. Three species - *Vellaria pellucida* Gooday & Fernando, 1992, *Psammophaga* cf. *simplora* Arnold, 1982 and *Bellarium rotundum* Anikeeva, Sergeeva & Gooday, 2013 – were found in collections from the Sea of Azov obtained in 2016-2017 during cruises on the Professor Vodyanitsky (Sergeeva, 2016; present). The analysis of the species composition of monothalamous soft-walled foraminifera of the Sea of Azov is continuing. The data presented above may form the basis for further, larger-scale studies of this group of organisms as an invariable component of the bottom communities of the Sea of Azov.

CHAPTER 10

PROTOZOANS IN BENTHIC FOOD WEBS AND AS POTENTIAL INDICATORS FOR THE SEDIMENTATION OF THE AZOV–BLACK SEA BASIN BOTTOM DEPOSITS

Soft-walled foraminifera and gromiids play an important role in the transmission of bacterial and algal production to the next trophic levels. From literature sources (Culver and Lipps, 2003; Lipps, 1983; Lipps and Valentine, 1970) and our own observations, we know that these protozoans are omnivorous, feeding on small bacteria, algae, pollen of terrestrial vegetation, hyphae and conidia of marine mycelial fungi, protozoa and multicellular invertebrates. In turn, they serve as an important food source for many benthic invertebrates in different habitats.

The distribution and abundance of foraminifera in general, and of soft-walled foraminifera in particular, in relation to food availability is of considerable interest. For example, Gooday and Turley (1990) and Gooday (1993) found that *Tinogullmia riemanni* Gooday, 1990 experiences periodic fluctuations in abundance associated with seasonal changes in food resources. This species typically occurs in benthic deposits of organic matter derived from surface production (phytodetritus) in abyssal areas of the north-east Atlantic (Gooday, 1990). Other evidence, however, suggests that allogromiids are less sensitive to such variations in organic matter than calcareous foraminifers, at least in deep waters (Gooday and Lambshead, 1989). For example, the population density of soft-walled foraminifera was 4.5 times greater in samples taken after the spring bloom than in samples taken before the bloom at a bathyal NE Atlantic site, while the quantitative development of calcareous foraminifera was 7.5 times greater (Gooday and Hughes, 2002). These differences in population densities may, in the authors' opinion, be due to contrasting responses of hard-shelled and soft-walled foraminifera to changes in the amount of organic matter in the environment, possibly related to differences in diet. Differences in the reproductive potential of the two groups are another possible reason.

Information in the literature on the nutrition of soft-walled foraminifera is scarce. In an experiment with samples from abyssal northeastern Atlantic using a pressurized incubation chamber, a small oval-shaped allogromiid with two apertures, similar to *Tinogullmia riemanni*, captured fluorescent microspheres the size of a bacterium (Turley et al., 1993). The cytoplasm of deep-sea allogromiids is often unpigmented and devoid of obvious food inclusions, indicating that they consume only very small particles, such as bacteria. Obviously, this conclusion applies only to deep-sea allogromiids.

It is noteworthy that monothalamous soft-walled foraminifera have been found in the remains of other organisms, in particular, in the molts of crustaceans, empty shells of calcareous foraminifers, and the organic tube systems of dead xenophyophores (Gooday, 1990; Hughes and Gooday, 2004; Moodley, 1990). This choice of microhabitat may be determined not only by the possibility of obtaining a reliable shelter, but also by the fact that large populations of bacteria accumulate in the remains of these organisms and serve as food for monothalamids.

The cytoplasm of other species contains large amounts of stercomata, which may indicate that they ingest sediment particles with bound organic matter (Gooday,

1986a). Thus, deep-sea monothalamids may be less dependent on inputs of new organic matter than calcareous foraminifera, many of whose species feed on fresh phytodetritus (Heeger, 1990; Turley et al., 1993).

There is also evidence of bacterial feeding among soft-walled foraminifera in shallow waters. Large populations of allogromiids are associated with the presence of dense populations of bacteria in Arctic coastal waters (Korsun and Hald, 2000). Direct evidence of bacterial ingestion by soft-walled foraminifera has been recorded in cultivated populations of *Allogromia laticollaris* (Muller and Lee, 1969; Bowser et al., 1985). Bernhard and Bowser (1992) observed *A. laticollaris* and *Allogromia* sp. that actively collected and absorbed bacterial biofilm under laboratory conditions. Bacterial feeding has also been observed in species such as *Cylindrogullmia alba* and *Nemogullmia longevariabilis* (Nyholm, 1953, 1974; Nyholm and Nyholm, 1975). In the case of *N. longevariabilis*, a large number of food vacuoles containing bacteria in different decompositional stages were found in the cytoplasm (Nyholm and Nyholm, 1975).

In addition, there is evidence in the literature that allogromiids are able to ingest particles larger than bacteria, particularly at shallow depths where food resources are diverse and readily available. Several species of soft-walled foraminifera, including *Rhynchogromia elegantula*, *Allogromia laticollaris*, *Gloiogullmia eurystoma*, *Hippocrepinella alba*, *H. hirudinea* and *Saccamina alba*, feed on diatoms and other relatively large food particles (Earland, 1933; Arnold, 1948; Nyholm, 1956, 1974; Gooday, 1986a; Goldstein, 1988; Golemansky, 1991). *Shepherdella taeniformis*, a filamentous allogromiid with two terminal apertures, feeds mainly on infusoria (Siddall, 1880). Plant fragments such as *Zostera* (Nyholm and Gertz, 1973) have also been observed in the cytoplasm of allogromiids.

Direct consumption of dissolved organic matter is another feeding mechanism that is used by some monothalamids. This has been demonstrated in experimental studies by DeLaca et al. (1981), Nomaki et al. (2011) and Tsuchiya and Nomaki, (2021).

A. Tchesunov et al., (2000) found a female and a male of the free-living nematode inside the shell of the monothalamous foraminifera *Vanhoeffenella* cf. *gaussi* Rhumbler, 1905. The nematode was described as a new species, *Smithsoninema inaequale* Hope & Tchesunov, 1999 (Hope and Tchesunov, 1999). This relationship between a multicellular organism and a protozoan is regarded by the authors as parasitism. We would venture to guess that the first stage of nematode colonization is primarily due to the availability of food resources contained within the foraminifera and the second stage is the use of the shell, which provides protection for the nematode during reproduction.

During microscopic analysis of the morphology of soft-walled foraminifera, we often note the presence of various objects (bacteria, sediment particles, crystals of unknown minerals, conidia and mycelial fragments of fungi, pollen of higher plants, diatom algae, macrophyte fragments, protozoa and metazoa fragments) inside the cytoplasm. We consider these as food particles or particles that contain food (Fig. 10.1). The spectrum of food particles within species such as *Psammophaga* sp. and *Bellarium rotundum* includes diatoms (i.e., algae) of the genera *Coscinodiscus* Ehrenberg, 1839 and *Navicula* Blainville, 1825. They are numerous and densely packed within the cell body of the SWF, although only one or two diatom species are

present, which suggests selective feeding. However, the integrity of the large and numerous ingested *Coscinodiscus* is surprising. Obviously, it takes a long time for the foraminifera to digest them. Unfortunately, this is only an assumption and is not confirmed by laboratory observations.

According to our observations of SWF, both allogromiids and saccamminids, are food objects for multicellular organisms, in particular free-living nematodes; examples of this can be seen in Fig. 10.1F-J.

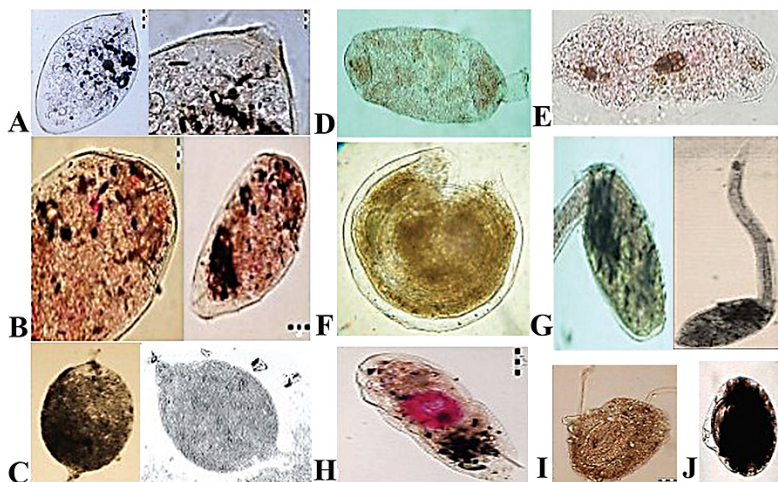


Figure 10.1. Representatives of soft-walled foraminifera with food objects in the cytoplasm: A-E - bacteria, diatoms, “fungi”; F-G – SWF specimens being preyed on by metazoans (nematodes); H-J – nematodes as food objects inside SWF (or SWF are food objects for nematodes) (by Sergeeva, 2019)

In the literature (Jiang et al., 2016; Hyde et al., 2014, Kopytina and Sergeeva, in press) is noted that invertebrates can be affected by fungi from the Divisions Mucromycota, Ascomycota, Basidiomycota, Chytridiomycota. Fungi-like organisms from the Oomycota and Hyphochytriomycota parasitize invertebrates. These fungal endophytes infect invertebrates in two ways: by spores that are eaten by animals and by spores adhering to the cuticle of animals. Infestation occurs mainly by fungi that are obligate parasites (saprotrophic fungi that live in the external environment and become parasitic when the animal is weakened).

We found interesting evidence of the use of soft-walled foraminifera as a substrate by organisms believed to be 'marine fungi' in the anoxic/sulfidic conditions of the Bosphorus area (252 m depth) and in the oxic environment of the north-western Crimean shelf (84 m depth) of the Black Sea (Fig. 10.2).

The fungi can only be identified by spores or genetic methods. Fungal spores are not visible inside immobile SWF, so the fungus-like organisms observed on the surface or inside soft-walled foraminifera remain of uncertain taxonomic status. However, we cautiously assume that these organisms belong to different fungal taxa.

In Fig. 10.2A, one kind of 'fungus' (we called it the 'star-shaped' form) probably penetrated through the aperture together with food into the cytoplasm of *Goodayia*

rostellata, apparently without interfering with the life activity of the monothalamid (Fig. 10.2A). However, it is difficult to conclude from this example whether these fungi are endoparasites or whether they serve as food. Other fungus-like organisms were found infecting the test surface of *Tinogullmia* sp., forming a dense coating or similar locally thickened areas on the wall (Fig. 10.2 B). Undoubtedly, this must cause the foraminifera to become immobilised and subsequently die (ectoparasites). Obviously, the fungi will continue to decompose this prey.

In Fig. 10.2C, a monothalamid identified as *Allogromiid* sp. is completely filled with a fungus-like organism different from those mentioned above. We assume that it has penetrated through the foraminifera's aperture without disturbing the test wall. The characteristic internal structure of the foraminifera has been largely destroyed, but the shape of the cell and its outer membrane are preserved. It is possible that this foraminifer died in situ, and the process of destruction and transformation by the fungus-like organism continued.

We hope that the connection that we have discovered between soft-walled foraminifera and possible fungi will attract the attention of specialists and serve as a starting point for further study of this phenomenon.

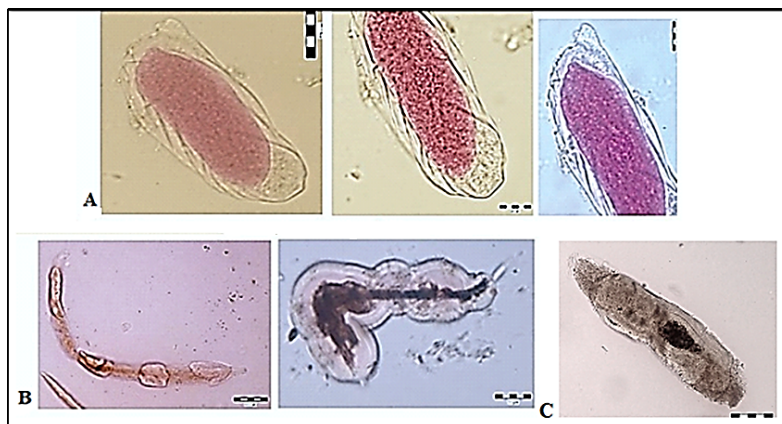


Figure 10.2. Possible marine fungi that infect SWF. A - general view of *Goodayia rostellata* with “fungi” in the anterior and posterior parts of the body; B - *Tinogullmia* sp. in a sheath of ‘fungi’; C - *Allogromiid* sp. - the entire cavity of the specimen is filled with parasitic “fungi”

Information on the selective capacity of soft-walled foraminifera of the genus *Psammophaga* Arnold, 1982 to accumulate specific minerals (magnetite, titanomagnetite, and zircon) in the cytoplasm was published during the past decade. *Psammophaga magnetica*, which contains magnetite and titanomagnetite crystals, was been identified in shallow bottom sediments of West Antarctica (Pawlowski & Majewski, 2011) and *Psammophaga zirconia* (Sabbatini et al., 2016), which accumulates zircon (51%) and titanium-bearing minerals (27%), was found in sediments of the central Adriatic Sea. *Allogromia crystallifera* was transferred to the genus *Psammophaga* based on the presence of intracellular mineral particles (Pawlowski and Majewski, 2011) (Fig. 10.3 A-C). The ability of *Psammophaga* species to selectively accumulate certain mineral in the cytoplasm makes these

foraminifera especially attractive for the analysis of their interactions with the environment.

Sabbatini et al. (2016) suggested that the selectivity for certain minerals by *Psammophaga* is species specific. Species-level differences among members of the genus *Psammophaga* most likely explain the ability to select and accumulate zircon and other heavy minerals, which provides an advantage for the persistence of the organism in the deposit and thus a more efficient trophic strategy. According to Sabbatini et al. (2016, pp. 414), "the presence of eukaryotic soft-walled monothalamous microfossils capable of building a thin aluminosilicate cover, in the geological record of the Precambrian makes them useful as a valuable record of early foraminifer evolution, suggesting that biological agglutination was already present in this group". The mechanism underlying the selectivity of foraminifera to minerals, however, remains unknown.

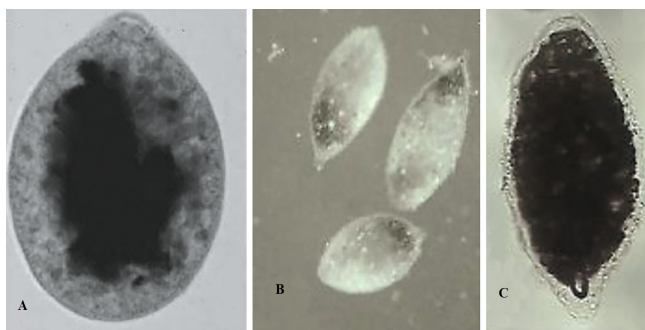


Figure 10.3. Three species of the genus *Psammophaga* with mineral crystals in the cytoplasm. A - *Psammophaga* cf. *crystallifera* Pawlowski & Majewski, 2011; B - *P. magnetica* Pawlowski & Majewski, 2011; C - *P. zirconia* Sabbatini et al., 2016 (by Sabbatini et al., 2016)

Species of the genus *Psammophaga* are common in the Black Sea and the Sea of Azov. The ability to accumulate crystals of minerals of an unknown nature is also characteristic of many other representatives of the SWF (Allogromiidae, Saccamminidae) in these seas (Sergeeva, 2019; Sergeeva and Anikeeva, 2018). More than ten *Psammophaga* and Saccamminidae morphospecies are represented in the author's collections, and black crystalline inclusions reminiscent of those previously described in *P. magnetica*, *P. crystallifera*, and *P. zirconia* (Pawlowski & Majewski, 2011; Sabbatini et al., 2016) were found in all cases. Almost all organisms with such inclusions found in the Black Sea and the Sea of Azov belong to Saccamminidae (Fig. 10.4A-H), but they are not yet described at the species level. As can be seen from Fig. 10.4, the distribution and packing density of crystals varies within the cells, but crystals tend to be most abundant in the anterior part of the cell. Further studies will reveal the composition of mineral crystals accumulated by these foraminifera.

The ability of some species of soft-walled foraminifera in the Black Sea and the Sea of Azov to accumulate mineral crystals of unidentified nature has not been noticed by researchers studying these basins. This may reflect the use of particular specific sample processing methods (e.g., drying) in paleontological studies of bottom sediments that lead to the destruction of delicate foraminiferal tests. The organic tests

of soft-walled foraminifera will decay after death but mineral crystals and diatom frustules will persist as millimetre-scale aggregations on the surface of, and within, the bottom sediments. These tiny concentrations of minerals may provide information about environmental conditions that could be relevant for the reconstruction of sedimentary basins during the past geological epochs.

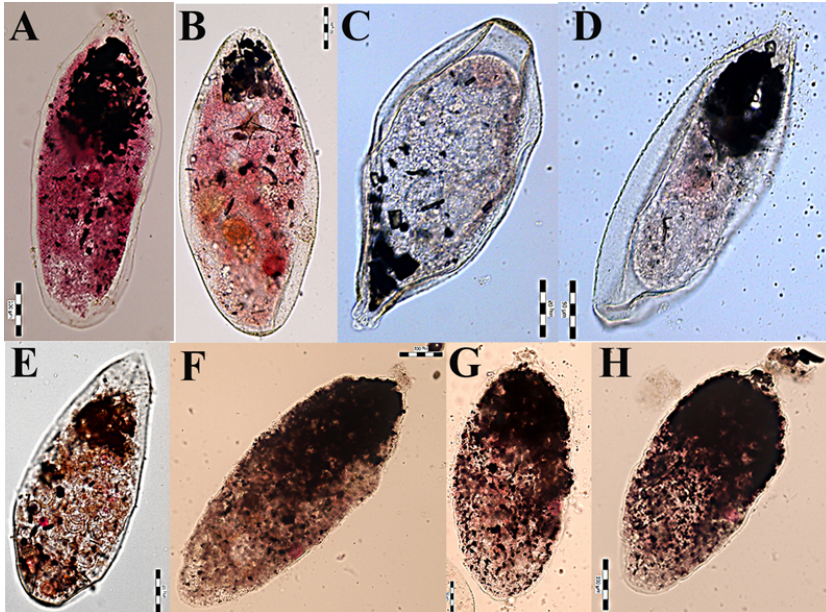


Figure 10.4. Soft-walled foraminifera of the Saccamminidae family (species are not identified) with distinct distributions of mineral crystals accumulated in the cytoplasm. Scale bar 50 μm (A–G, I–J, L), 100 μm (H, K).

Meiofauna play important intermediary roles in the cycling of nutrients in deep-sea settings (e.g., Soltwedel, 2000; Gooday, 2002). The ecological role of gromiids is poorly known but they are probably involved in the cycling and decomposition of organic matter on the seafloor in areas where they are abundant (Gooday et al., 2000a, b; Gooday, 2002; Pawlowski et al., 2005). We have no information on the nutritional requirements of *Gromia*, but they are often associated with carbon-rich sediments and probably feed on phytodetritus and other more degraded organic matter (Rothe et al., 2011). The apertures of the gromiids are directed downwards towards the sediment surface and, like foraminifera, they use their pseudopodia for feeding (Rothe et al., 2009; Aranda da Silva and Gooday, 2009). Stercomata, extracellular waste pellets, as well as mineral grains that are accumulated inside the cell, are a characteristic feature of *Gromia*. The stercomata consisting of small clay mineral grains and undigested waste.

Like some foraminifera, gromiids have been shown to store nitrate. Intracellular nitrate concentrations can reach >100 mM in gromiids, which exceeds the ambient nitrate concentration by several orders of magnitude (Piña-Ochoa et al., 2010). Høgslund et al., (2017) showed that nitrate concentration ranges from 1 to 370 mM

and can exceed those in the environment by up to 1000 times. The ability to accumulate nitrate at these high concentrations appears to be ubiquitous for the gromiids (Kamp et al., 2015). Significant stores of nitrate are stored inside the living cells of several benthic marine taxa. The fate of this bioavailable nitrogen varies according to the organisms controlling intracellular nitrate. In gromiids, it has been suggested that high levels of intracellular nitrate are used in respiration, a process leading to the release of nitrogen gas through denitrification (Piña-Ochoa et al., 2010). However, the physiology of gromiids has been studied only superficially and neither the mechanism behind nitrate accumulation, nor its link to any metabolic pathway has been investigated so far. It is possible that the gromiid-nitrate association represents a system that is functionally different from that of benthic foraminifers because gromiids generally are described as surface dwellers, and thus not buried in anoxic sediment layers like many foraminifers (Jepps, 1926; Hedley and Bertaud, 1962; Arnold, 1972; Gooday et al., 2000 a, b; Gooday and Bowser, 2005; Matz et al., 2008; Aranda da Silva and Gooday, 2009; Rothe et al., 2011).

Based on our own observations, it is important to note (as in Chapter 6) that the cytoplasm of some gromiid species are filled with endosymbionts (Symbiodiniaceae), fragments of multicellular organisms (harpacticoida, oligochaeta, polychaeta), pollen from higher terrestrial plants, diatoms, fungal hyphae and conidia (Fig. 10.5).

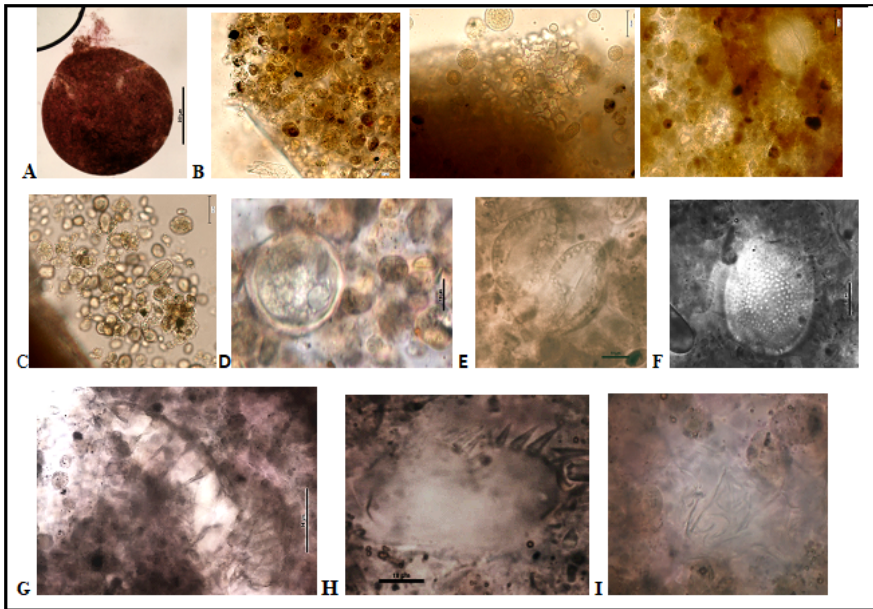


Figure 10.5. Representatives of gromiids with food particles and other cytoplasmic inclusions. A – general view of gromiids, B-C – microphyte endosymbionts; D-F – pollen and diatom frustules; G-I – metazoan fragments inside gromiids.

CONCLUSION

Soft-walled foraminifers and gromiids are poorly studied in the Black Sea and the Sea of Azov. The latest summary of modern foraminifers of the Bulgarian shelf (Temelkov, Golemansky and Todorov, 2006) includes six representatives, two of which are identified only up to the genus. According to our unpublished data, *Psammophaga simplora* reaches its highest quantitative development on the Bulgarian shelf (Varna Bay) at depths of 70-100 m. Based on our own data, and those available for the Bulgarian coastal zone (Temelkov, Golemansky and Todorov, 2006; Golemansky, 1974; Golemansky, 1999a, b), we conclude that the Black Sea soft-walled foraminifera are much more diverse and distributed across a wide range of depths. However, some species are confined to specific regions, depths and biotopes, while others are eurybiontic forms.

Psammophaga cf. simplora, in particular, has a wide geographical distribution in the Black Sea. According to our data, it occurs on the shelves of Bulgaria, the Caucasus, Türkiye, western, south-western and southern Crimea (Tarkhankut, Donuzlav Bay, Sevastopol and Laspi bays) and in the Sea of Azov. This species dominates the meiobenthos at depths of 142-260 m to the south-west of the Crimean Peninsula, reaching a population density of 86-116,000 individuals/m². Soft-walled foraminifera, mainly *Psammophaga sf. simplora*, are among the meiobenthic subdominants in the area of methane gas seeps at a depth of 77-172 m, again to the south-west of the Crimean Peninsula (Sergeeva, 2003; Revkov and Sergeeva, 2004). *Vellaria pellucida* and *V. sacculus* are also widespread in coastal waters. In the areas we studied, these species are among the most frequent and occur in fine sand and muddy substrates with a high population density (up to 110,000 individuals/m² and higher).

The study of this group of organisms is far from complete and new species are expected to be identified and described in the future. However, on the basis of the data we have presented, we can state that soft-walled foraminifera are highly diverse and numerous and play an important role in the cycling of substances in the bottom ecosystems of the Black Sea and the Sea of Azov. They are adapted to different habitats up to the extreme hydrogen sulfide conditions and anoxia.

Currently, the soft-walled foraminifera of the Black Sea comprise 13 valid species, dozens of morphospecies and morphotypes, identified only to the level of genus or family, requiring further detailed study. The soft-walled foraminifera of the Sea of Azov include 3 valid species and more than 10 morphotypes that require further detailed study. The taxonomic richness of soft-walled foraminifera therefore makes a significant contribution to the overall biodiversity of the Black Sea and the Sea of Azov. SWF also constitute a significant proportion (up to 75%) of the total density of meiobenthic communities.

Even less is known about Black Sea gromiids. According to our preliminary data, the genus *Gromia* is represented in the Azov-Black Sea basin by at least 10 morphotypes. They are known to inhabit not only mussel collectors (Syrtlanova and Anikeeva, 2007) but also soft sediments in shallow water (Sergeeva and Anikeeva, 2006). In the area of the Istanbul Strait (Bosporus) (depths 75-300 m) gromiids account for a significant proportion of the total number of meiobenthos both in normoxic and acute hypoxic settings down to the anoxic/hydrogen sulfide zone

(Sergeeva et al., 2012, 2013, 2015, 2017; Sergeeva and Ürkmez, 2017). They also inhabit bottom sediments enriched with methane seeps in the oxic-anoxic zone of the Dnieper Paleo-Delta (Sergeeva and Gulin, 2009).

Our earlier results (Sergeeva et al., 2017), and new data presented in the present work, showed that benthic protozoans are a consistent and integral component of meiobenthic communities under different environmental conditions in the Black Sea. Conducted studies on main taxa of meiobenthic communities at different depths and regions of the Black Sea allow us to give an overall picture of the distribution and the reaction of protozoans to the environment, establishing a link between different taxa and suggesting their important role in benthic ecosystems. As the water depth increases in the Black Sea, the biodiversity and abundance of macrobenthos decreases and the contribution of protozoa to benthic ecosystems becomes higher. However, we also observed considerable inconsistencies between the spatial and bathymetric distribution of protozoans and metazoans.

Changes observed in the taxonomic composition and contribution of different protozoan taxa to the total meiobenthos depend on various factors. They may be related to particular aspects of the small-scale distribution and availability of food resources, the number of macrobenthic fauna and their bioturbation activities, and changes in levels of oxygenation from oxic to anaerobic conditions with high concentrations of hydrogen sulfide. We assume that some protozoan taxa are adapted to such conditions and can attain high population densities. Protozoans are significant components of benthic communities since they are an important food source for animals at higher trophic levels. They are consumers of bottom bacteria, microalgae, terrestrial pollen and marine filamentous fungi; they may also prey upon unicellular and multicellular organisms as predators, as well as assimilating dissolved organic matter. Anaerobic bacteria decompose organic material under conditions of hydrogen sulfide in the Black Sea, and the final products are sulfates. These bacteria, in turn, are a food source of many benthic protozoans. In addition, protozoans form part of the diet of many benthic invertebrates inhabiting various habitats. Protozoans play a particular role in terms of oxygen depletion, thanks to symbiotic relationships with *Cryptobiontes*-like and *Symbiodinium*-like (Dinophyta) organisms, and they participate in the cycling of organic matter in benthic ecosystems in oxygen-depleted environments, where other organisms are scarce.

These data underline the need to study the species diversity of protozoans inhabiting different habitats. There are undoubtedly particular species of ciliates, foraminiferans and gromiids that are confined to extreme habitats, in addition to widespread forms. Based on the data obtained, we conclude that the benthic protozoans are important components of benthic communities and their role in the functioning of Black Sea benthic ecosystems needs to be investigated. In this context, we studied certain characteristics of protozoan communities (bathymetric and spatial distribution, abundance, and ratio of main taxa) as a component of whole meiobenthic assemblages.

In this publication, we summarise for the first time existing and original data on the main benthic protozoan taxa and changes in their contribution to meiobenthic communities under conditions ranging from normoxia to anoxia in the Black Sea. Future research should focus on their species diversity and understanding the role of each protozoan species or group in benthic ecosystems, links between different taxa

and their relationship with the environment. The data we present suggests that eukaryotic life is present in anoxic Black Sea waters and sulfidic sediments which have been considered as “toxic” environments. This result is consistent with the data about the potential for anaerobic metabolism in many protozoans (Esteban, Fenchel, 2020; Massana and Pedros-Alio, 1994). It is possible now to refute the view that the Black Sea is lifeless at depths containing hydrogen sulfide by direct observations of active protozoans and metazoans, living in the deep-water hydrogen sulfide zone (Sergeeva et al., 2014). Additionally, two species of epibiont peritrich and suctorian ciliates living on benthic animals have recently been described at a depth of 253 m under anoxic conditions enriched with hydrogen sulfide (Sergeeva and Dovgal, 2014, 2016). Further studies will be necessary to reveal the factors regulating the abundance of benthic protozoans and metazoans at the oxic-anoxic interface of the Black Sea, to identify the origin of specific deep-water communities, their diversity and role. Hypoxia poses many difficulties for aerobic organisms and leads to changes in the structure of benthic communities and a reduced biological diversity. Extreme conditions also eliminate a number of aerobic benthic forms. Our data suggest that the oxic/anoxic transition zone supports dense and diverse meiobenthic assemblages and particularly protozoans (Gromiida, Ciliophora and Foraminifera), which are the most abundant representatives of the eumeiobenthos in samples from deeper, anoxic/sulfidic areas of the Black Sea.

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