

**ORIGIN, PHYLOGENETIC RELATIONS, AND ADAPTATIONS  
OF THE MARINE INTERSTITIAL TESTATE AMOEBAE  
(RHIZOPODA: LOBOSEA, FILOSEA, AND GRANULORETICULSEA)**

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*Abstract* — After a brief historical review of studies on the marine interstitial testate amoebae, an ecological characterization of their specific habitat is given. The author's hypotheses about the origin and phylogenetic relations of the marine interstitial testate amoebae are based on morphological studies only. Most of the currently known marine interstitial testate amoebae are phylogenetically related to widespread freshwater and soil testate amoebae. The number of lobose testate amoebae is limited to about 15 species in the marine habitat, where filose testate amoebae predominate with more than 45 species. Several marine interstitial testate amoebae from the genera *Lagynis*, *Lagenidiopsis*, and *Rhumbleriella* are phylogenetically related to monothalamous foraminifera. Some morphological and biological adaptations of the marine interstitial testate amoebae to their specific habitat are also discussed.

*Key words*: Rhizopoda, marine testate amoebae, origin, phylogeny, adaptations

INTRODUCTION

For a long time, the dominant opinion in protozoology was that the testate amoebae are exclusively freshwater inhabitants. They were considered to be freshwater equivalents of the widely distributed and abundant marine foraminifera. Sparse data indicating the presence of some testate amoebae in different marine habitats were published by Shulze (1874), Gruber (1884), Mobius (1889), Buchinskii (1895), Awerintzew (1903), etc., but the observed species were considered to be freshwater inhabitants that occasionally drifted into the sea from continental freshwaters.

Wailes (1927) was the first researcher to investigate in detail interstitial marine protozoans, which he found in the sand supralittoral of the Pacific (British Columbia). In groundwater of the sand beach of Camp Island near Vancouver, he observed three species of testate amoebae, one of which he described as a new taxon – *Corythion acutum* Wailes, 1927. At that time, he did not presume the new species to be a member of a specific marine testacean taxocenosis and concluded: “Although found on the sea shore, as described below, it is in all probability a freshwater or moss-inhabiting species”. That is why Wailes (1927) placed the new species in the

freshwater genus *Corythion* Taranek, 1881. The other two testate amoebae observed by Wailes in the same habitat were *Cyphoderia ampulla* and *Euglypha laevis*, which he also considered to be freshwater testate amoebae carried out from continental underground freshwaters. More than 25 years later, Valkanov (1954) observed the same *C. acutum* in the underground water of some Black Sea sand beaches (Varna, Pomorie, Sozopol, etc.) and noted that the species inhabits “the same ecological habitat” as in the Pacific. In conclusion, he also postulated that the testate amoebae observed in the marine habitat were freshwater species occasionally carried there.

As a result of more detailed studies on interstitial testate amoebae of the sand supralittoral of the Black Sea initiated after 1966, there were established and described many new and unknown genera and species of this group, proving the existence of a specific interstitial psammobiotic taxocenosis in the sea littoral (Golemansky, 1969, 1970a, 1970b, 1970c, 1970d, 1970e; Valkanov, 1970). Over the next decades, this taxocenosis of psammobiotic interstitial testate amoebae was proved to exist in many other seas and oceans in the world by Chardez (1971, 1972a, 1972b, 1977, 1978), Laminger (1973), Decloitre (1972, 1975), Sudzuki (1977a, 1977b, 1979), etc. Golemansky (1974) described the new family Psammonobiotidae for the specific inhabitants of this taxocenosis, its members possessing characteristic morphological and biological adaptations to the marine interstitial habitat.

The establishment of the common and widespread marine interstitial testate amoeba *Psammonobiotus communis* in the littoral sand sediments of Lake Ohrid was an interesting fact. It was considered as a marine relic in the tectonic Lake Ohrid, which arose from the old Sarmatian Sea (Golemansky, 1970b).

At present more than 120 species of testate amoebae have been established in

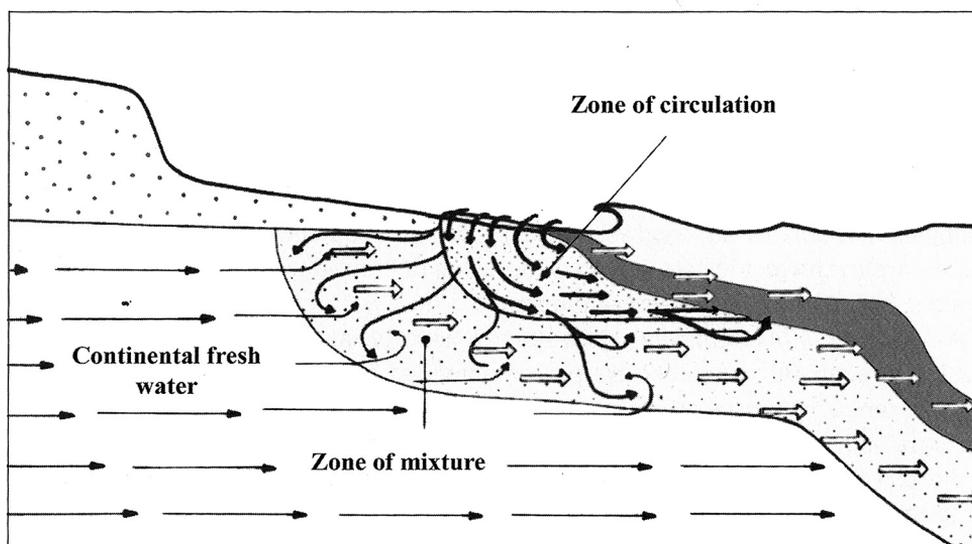


Fig. 1.

the studied seas and oceans. They belong to three ecological categories: obligatory or strict psammobionts (about 80 species), psammophiles (about 10), and psammoxenes (more than 30 species). More detailed studies on their morphology and ultramorphology, geographic distribution, ecological preferences, and biological features have been carried out to date by many authors. These studies indicate that psammobiotic testate amoebae possess some specific morphological and biological adaptations to the interstitial habitat (Golemansky, 1978, 1986, 1990; Golemansky and Couteaux, 1982; Golemansky and Todorov, 2004; Todorov and Golemansky, 2006; Ogden and Couteaux, 1989; etc.).

Despite progress in study of the morphology, taxonomy, and ecology of the marine interstitial testate amoebae, the problem of their origin and phylogenetic relations to the freshwater testate amoebae or the marine microforaminifera has not been satisfactorily discussed so far. The aim of this paper is to present our viewpoint on the origin and phylogenetic relations of marine interstitial testate amoebae to some recent freshwater and marine rhizopods and their main morphological and biological adaptations to the interstitial habitat.

#### THE PSAMMAL MARINE SUPRALITTORAL AS A SPECIFIC HABITAT

According to the classification of Perez and Picard (1958), the sea bottom can be divided into the following seven zones, arranged from land to sea:

The supralittoral, situated above the sea's water line. The inhabitants of this zone are mainly of continental origin, and the number of the marine organisms is limited.

The mediolittoral (eulittoral), situated on the boundary between land and sea, its width depending on the sea's ebb and flow. The creatures there are mainly of marine origin, but some freshwater organisms also occur, and they often have various characteristic morphological adaptations to the zone's specific ecological conditions.

The next five zones of the sea bottom are the infralittoral, circalittoral, batial, abyssal, and hadal, and their inhabitants are of marine origin only.

Marine interstitial testate amoebae mainly inhabit groundwater in the supralittoral and partially occur on mediolittoral sand beaches, where an active mixture of continental freshwater and seawater is present. According to Swedmark (1964), this unstable habitat can be considered to be a transitional zone between continental freshwater and seawater. In continental seas such as the Black Sea, which lack a well-expressed ebb and flow, the transitional zone (or mixed zone) is relatively constant, and there is regular mixing of continental freshwater and sea-water (Fig. 1).

Width of the mixed zone between the continental underground freshwater and seawater depends mainly on the velocity of penetration of continental water. This zone is larger on sand beaches with a limited flow of continental freshwater and is virtually absent or is limited on beaches where the freshwater flow is massive and rapid. Also, width of the given zone is not constant during the year and depends on seasonal and annual rainfall, wind direction and intensity, the degree of roughness of the sea, and many other factors.

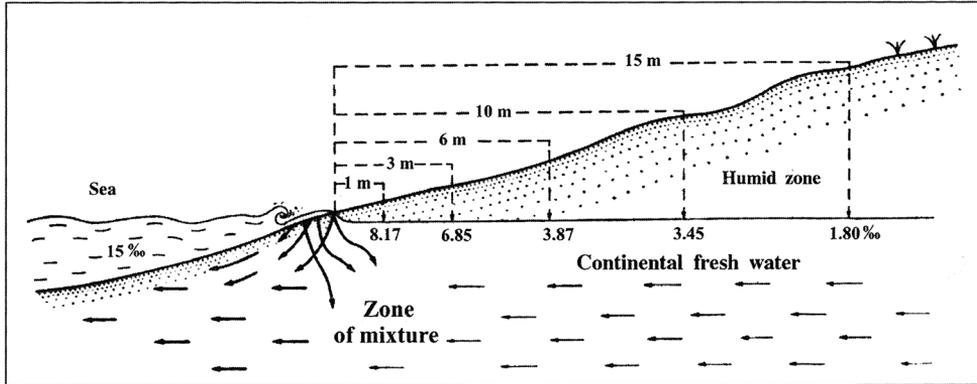


Fig. 2.

As an important ecological factor, water salinity is also variable in the transitional zone of mixture and fluctuates within wide limits. Near the seashore (0-3 m from the water line), the salinity of underground water is higher and its value is almost the same as that of seawater (30-35% for normal seas, 15-18% for the Black Sea, 5-7% for the Baltic Sea), but salinity values in the highest sand zone decrease to 2-0.5% (Golemansky, 1980). Coineau (1970) notes that salinity in the zone of water mixture can change quickly – from 7.25% to 37.2% in a few hours during rough seas and its values are higher in summer than in autumn and winter. Changes in salinity of the underground water on a Black Sea beach from sea to land are shown in Fig. 2.

The water level in shore sand sediments is also variable and depends on declination of the seashore, dimensions and form of the sand grains, seasonal and climatic conditions, etc. As a rule, the underground water level on the same sand beach is higher during rain storm or torrential spring rain and noticeably lower during the summer months of the year. Fine sand sediments ( $M_o = 0.1-0.4$  mm) retain a higher water level than coarse heterogeneous sand sediments ( $M_o = 0.5-1.6$  mm). It is important to note that in the distal zones of sand beaches the interstices between the sand grains are often filled by detritus or argillaceous particles carried by continental underground water, and that oxygen there (as an important ecological factor) is very limited or completely absent. Such anoxic sand sediments and underground water lack interstitial testate amoebae.

#### ORIGIN AND PHYLOGENETIC RELATIONS OF MARINE INTERSTITIAL TESTATE AMOEBAE

Regardless of the fact that testate amoebae have been studied for more than 250 years, their origin and phylogenetic relations with the other close taxonomic groups are not clear enough. The dominant opinion is that they are an ancient group of protists with polyphyletic origin that arose from the large and heterogeneous group

of naked amoebae. De Saedeleer (1934) considers the family Cochliopodidae to be primitive predecessors of the lobose testate amoebae and phylogenetically related to the naked lobose freshwater amoebae. Page (1976) wrote that the flexible coating of Cochliopodidae “makes them disputed territory between Gymnamoebia and Testacealobosia (lobose amoebae with testa)...”, and it is possible that the filose testate amoebae are phylogenetically related to filose naked predecessors. De Saedeleer (1934) considers the naked filose amoebae of the genus *Penardia* to be possible predecessors of testate amoebae of the group Testaceafilosia. In the so far generally accepted “A Newly Revised Classification of the Protozoa” (Levine et al., 1980), the testate amoebae *sensu lato* were placed in the superclass Rhizopoda von Siebold, 1845 and especially in the classes Lobosea Carpenter, 1861; Filosea Leidy, 1879; and Granuloreticulosa De Saedeleer, 1934. Recent investigations on the phylogenetic lineages of eukaryotes by molecular and genetic methods show that these traditional systematic groups are no longer valid, and a new improved classification was recently proposed (Adl et al., 2005). In the new classification, the testate amoebae are placed in two different clusters: Amoebozoa (Luhe, 1913) Cavalier-Smith, 1998 (with amoeboid locomotion by morphologically variable pseudopodia or lobopodia) and Rhizaria Cavalier-Smith, 2002 (with fine simple, branching, or anastomosing filopodia, or axopodia). But this newly proposed classification is not accepted so far without reservation by many protistologists and requires more detailed investigations in order to be confirmed.

To approach the problem of the origin and evolution of the testacean taxocenosis in marine sand supralittoral groundwater solely on the basis of morphological and ecological criteria is a risky undertaking, because of the insufficient knowledge of the group at present. In the first place, marine interstitial testate amoebae have been the object of limited studies only for the last forty years. Secondly, there are no detailed studies on their phylogeny based on multigenic sequence data. Therefore, the present contribution is a preliminary attempt to discuss the origin and phylogeny of marine interstitial testate amoebae based only on their morphology and their similarities with known freshwater and marine rhizopods.

The number of lobose testate amoebae observed so far in the marine interstitial habitat is limited to only about 15 species. Six of them are strict psammobionts belonging to the freshwater genera *Diffugia*, *Cryptodiffugia*, and *Diffugiella*: *Diffugia subterranean*, *D. submarina*, *Cryptodiffugia lanceolata*, *C. paludosa*, *C. brevicolla*, and *Diffugiella psammophila*. They are all morphologically similar to widespread freshwater species of the cited genera and we consider that they are phylogenetically related to them. In marine supralittoral groundwater, they are represented by one or several species, but in freshwater, moss, and soil habitats there are dozens of species and varieties. We note that more than 100 valid species of the genus *Diffugia* are known so far from different freshwater habitats, but only two that inhabit the marine sand supralittoral.

A particular case is *Pomoriella valkanovi*, which is characterized by its flask-shaped shell, with non-overlapping siliceous rectangular plates and well-expressed

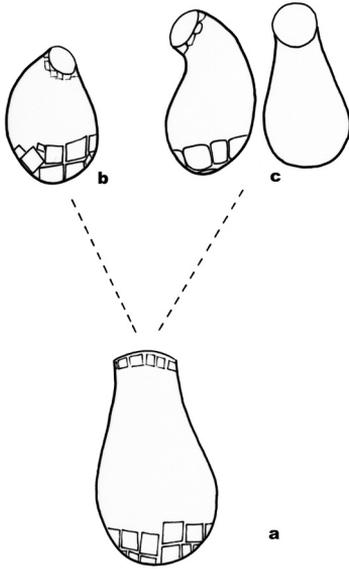


Fig. 3.

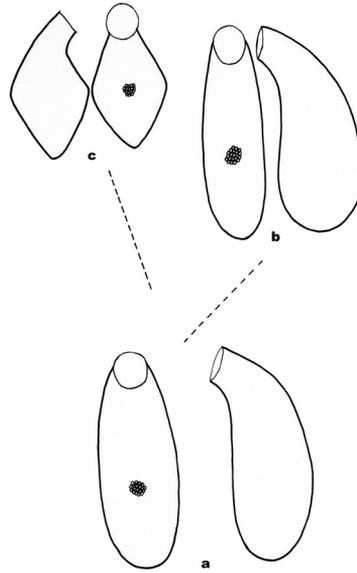


Fig. 4.

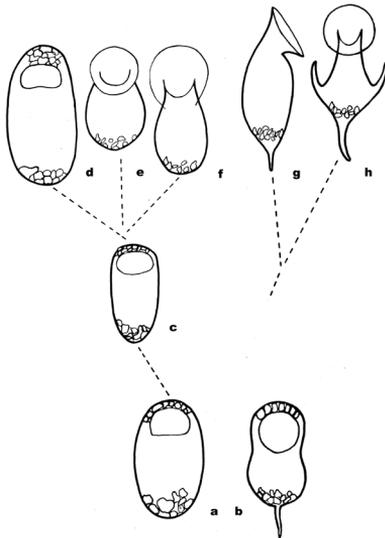


Fig. 5.

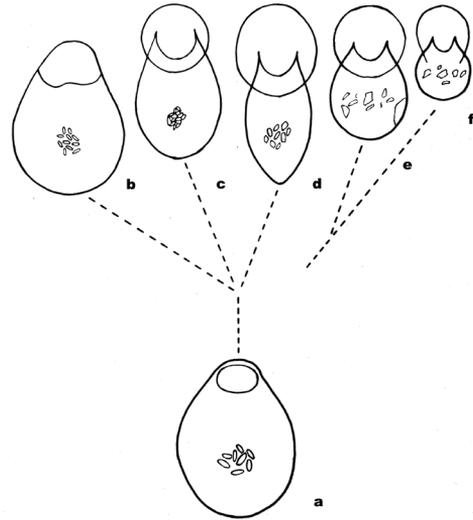


Fig. 6.

lobopodia. So far, it is the only known marine inhabitant from the family Lesquereusidae. In the same family, four other genera are known: *Lesquereusia*, *Netzelia*, *Quadrulella*, and *Microquadrula*. In regard to shell morphology, the monospecific genus *Pomoriellia* is very close to *Quadrulella* and *Micriquadrula*, and we suppose that they are phylogenetically related (Fig 3). The most widely distributed in

different freshwater habitats are species of the genus *Quadrullella*, and we consider that some of them are predecessors of *Microquadrulla* and *Pomoriella*. Both genera are monospecific: *M. muscifila* inhabits moss on rocks and *P. valkanovi* is a psammobiotic form. The morphological similarity of *P. valkanovi* with some species of the genera *Paraquadrula* and *Lamptoquadrula* is due to convergence, since their shells are formed by calcite plates rather than siliceous ones, as in *P. valkanovi*.

The majority of testate amoebae inhabiting the marine sand supralittoral have filose pseudopodia and form part of the order Euglyphida (Meisterfeld, 2000). Sufficiently clear phylogenetic relations exist between them and freshwater and marine interstitial species of the family Cyphoderidae. From the widespread genus *Cyphoderia*, more than 20 species and varieties have been described from freshwater habitats and only three from the marine sand supralittoral: *C. ampulla*, *C. littoralis*, and *C. compressa*. *C. ampulla* is eurybiont found in both freshwater and marine habitats, but *C. compressa* and *C. littoralis* are strict psammobionts which we consider to be descended from some freshwater predecessors, probably from *C. ampulla* (Fig. 4).

Phylogenetic relations of the widespread interstitial testate amoebae of the genera *Centropyxiella*, *Micropsammella*, and *Alepiella* are relatively clear. They all have an evaginated shell periphery in the region around the aperture, but their shell structure is very close to that in members of the freshwater, moss-dwelling and soil-inhabiting genus *Centropyxis*, which includes more than 120 species and varieties worldwide (Fig. 5).

Another psammobiotic testate amoebae group, represented by more than 15 widespread marine interstitial species, is the group *Psammonobiotus-Corythionella*. The shells of *Psammonobiotus* species are formed of an organic matrix with some polygonal organic plates (idiosomes) of different size, while the shells of *Corythionella* species are formed by numerous elliptic or rarely irregular idiosomes with the same form and arrangement as in the freshwater genus *Corythion*. That is why we consider that both psammobiotic genera are phylogenetically related to the freshwater *Corythion* species (Fig. 6).

With respect to shell structure, marine interstitial testate amoebae of the genera *Pseudocorythion* (four species) and *Messemvriella* (one species) are very close to species of the genus *Trinema*. To the same group we add the strictly marine psammobiont *Chardezia caudata*, whose shell is similar in form to that of *Pseudocorythion acutum*, but in which the idiosomes have shape that is variable and intermediate between *Corythionella* and *Pseudocorythion*. Possible phylogenetic relations between the freshwater *Trinema* and interstitial testate amoebae of the genera *Messemvriella*, *Pseudocorythion*, and *Chardezia* are illustrated in Fig. 7.

The interstitial testate amoebae with acrostom shells represent a relatively small group with about 12 species of three genera: *Pseudodifflugia*, *Ogdeniella*, and *Micramphora*. So far, the genus *Pseudodifflugia* includes about 20 species, the majority of which are freshwater inhabitants, only four species having been registered in the marine interstitial habitat. One of them (*P. fascicularis*) has often been observed

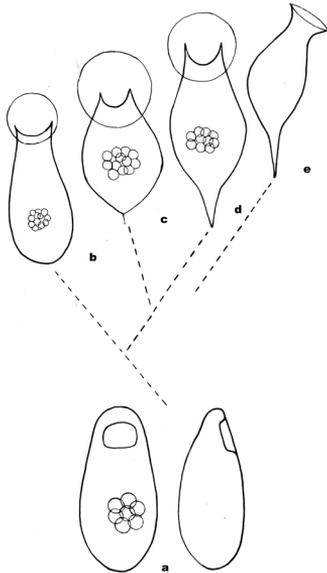


Fig. 7.

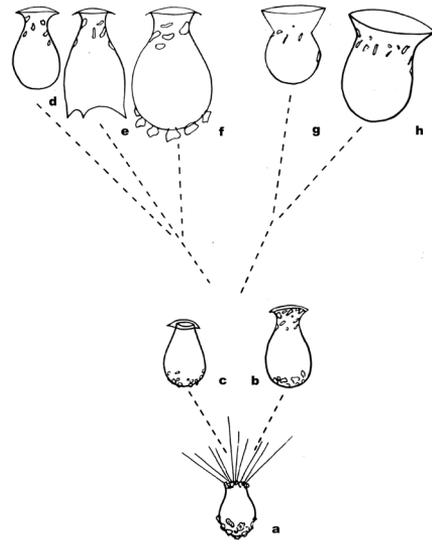


Fig. 8.

in underground water of the Black Sea shore and we consider it too a psammophilic inhabitant. The genus *Pseudodifflugia* is also close to the freshwater genus *Nadinella*, described from Lake Lemán (Switzerland). The other two strictly psammobiotic genera – *Ogdeniella* and *Micramphora* — are nicely characterized by the presence of a funnel-like collar around the aperture. Based on shell form and structure, as well on the type of their pseudopodia, we consider that all the cited genera constitute a branch of the same phylogenetically related group (Fig. 8).

The above-discussed marine interstitial testate amoebae are closely related to different widespread freshwater testate amoebae, and in general we accept that they are phylogenetically related to them. In their given habitat, they have acquired some specific morphological and biological adaptations enabling them to live there, but their basic taxonomic characters are the same or very close to those of their freshwater antedents.

In groundwater of the psammal supralittoral marine live some other rhizopods with unclear phylogenetic relations, for example *Lagenidiopsis valkanovi* and *L. elegans*, *Rhumleriella filosa*, *Lagynis pontica* etc. (Fig. 9). They all are of undoubtedly marine origin and are probably phylogenetically related to marine foraminifera and more precisely to the group of monothalamous foraminifera (Fig. 10).

#### MORPHOLOGICAL AND BIOLOGICAL ADAPTATIONS TO THE SPECIFIC HABITAT

In general, the known testate amoebae so far number about 1500 species and subspecies, which can be divided into four ecological categories:

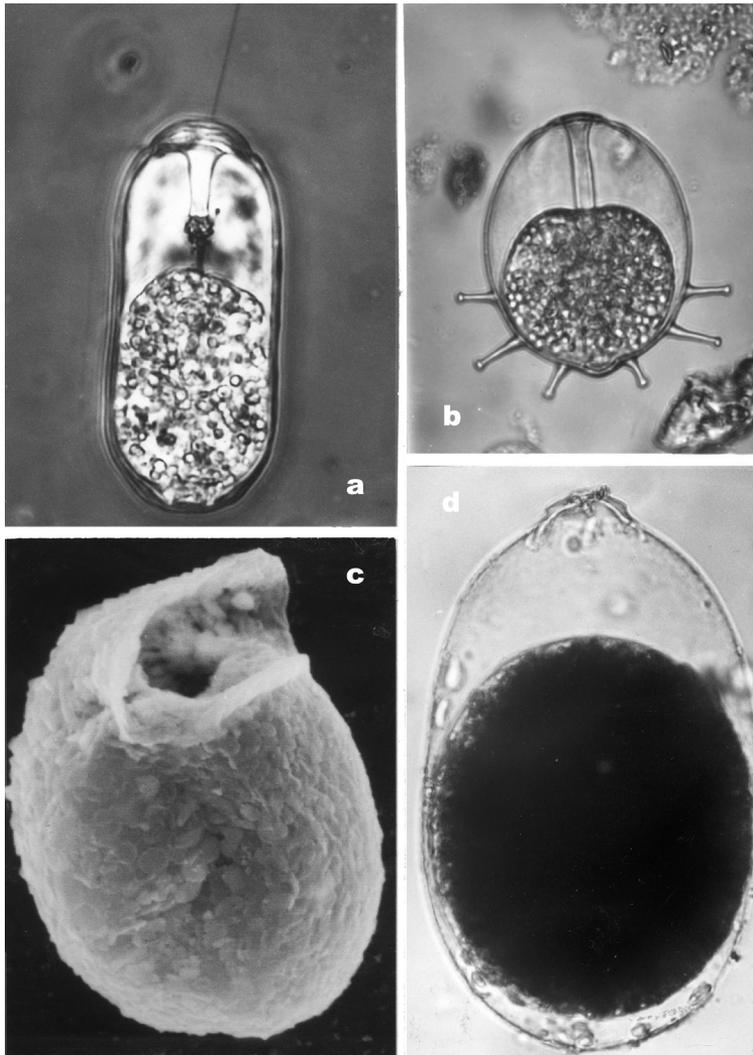


Fig. 9.

- Freshwater-dwelling — these inhabit various lakes, marshes, rivers, springs, and other freshwater basins. More than 50% of the known testate amoebae belong to this category;

- Moss-dwelling — these inhabit peat bogs, rocky moss, soil, and epiphytic moss. This category includes about 30% of the known testate amoebae;

- Soil-dwelling — these inhabit different types of soil, including the forest leaf layer and superficial humus layer (Ao, A1). About 15% of currently known testate amoebae belong to this category, and some of them are good bio-indicators;

- Marine-dwelling — these mainly inhabit the marine littoral and sea-linked salt-water lakes with varying salinity. They constitute only about 4-5% of the known

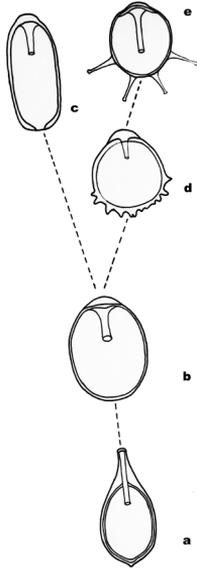


Fig. 10.

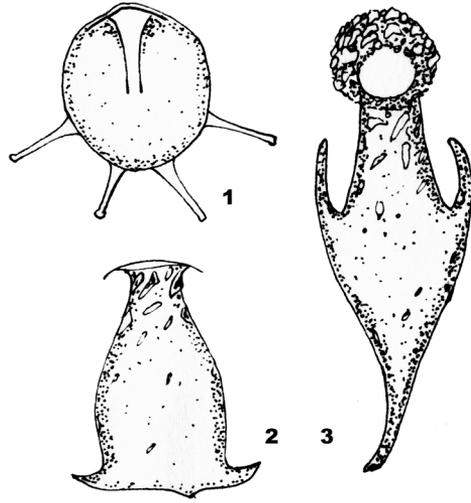


Fig. 11.

testacean taxa and mainly inhabit underground water in large supralittoral sand bands, i.e., they belong to the category of the marine interstitial fauna or to the *psammon* (Zassouchin, 1931).

It should be noted that there are no strong boundaries between the four ecological categories mentioned above: often some species can be observed in two or more different habitats, as in the case of some cosmopolitan eurybionts such as *Trinema lineare*, *Euglypha loevis*, etc.

The characteristic testate amoebae from the indicated ecological categories possess different morphological, biological, and ecological adaptations to their specific habitats. The morphological and ecological adaptations to their habitats exhibited by typical freshwater, soil-inhabiting and moss-dwelling testate amoebae have been studied best (Deflandre, 1953; Thomas, 1959; Bonnet, 1961, 1964, 1975; Schonborn, 1964, 1999; etc.). Little is known about adaptations of the marine testate amoebae, owing to their late discovery and insufficient investigation up to now (Golemansky, 1969, 1978, 1980; Chardez, 1972).

The main morphological adaptations of marine interstitial testate amoebae to their specific habitat – the underground water of sand beaches – are as follows:

1. Reduced shell dimensions in comparison with freshwater and humid moss-dwelling testate amoebae. According to our previous verifications, more than 75% of the known psammobiotic testate amoebae have small and delicate transparent shells with shells measuring between 15 and 60  $\mu$ . The shells of very few of them measure between 60 and 100  $\mu$ , and only three psammobiotic testate amoebae (*Lagynis pontica*, *Lagenidiopsis elegans*, and *Cyphoderia compressa*) have shells measuring more than 100  $\mu$  (Golemansky, 1978).

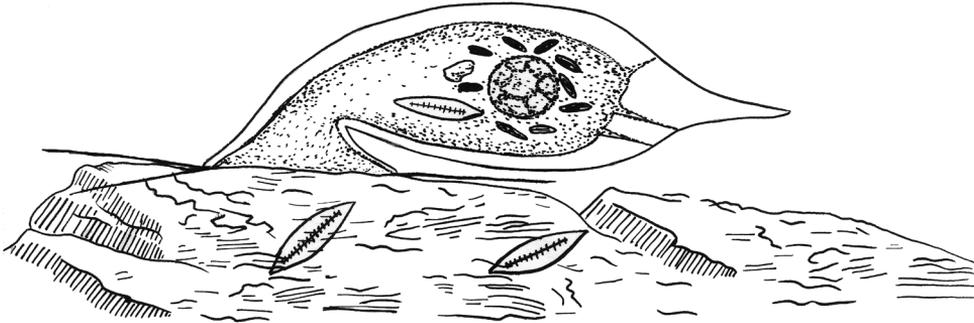


Fig. 12.

2. Presence of laterally or dorso-ventrally compressed shells. This morphological peculiarity was observed in about 50% of the studied marine interstitial testate amoebae. In general, few interstitial testaceans have shells that are round in cross section, and their shells are small and never measure more than  $60\ \mu$  (illustrative examples include *Micramphora pontica*, *Diflugiella psammophila*, *Psammonobiotus linearis*, *Ogdeniella lucida*, etc.).

3. Organic translucent shells, rarely covered by organic plates or mineral particles (xenosomes), disposed mainly in the region of the aperture or in the shell base.

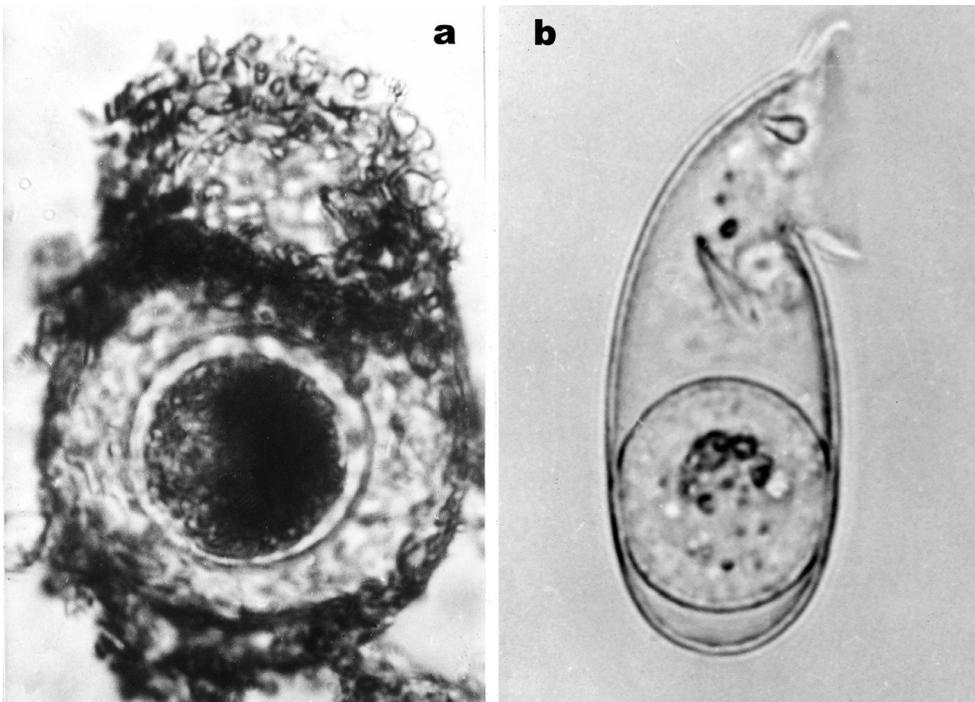


Fig. 13.

Several psammobiotic testate amoebae have organic shells without clearly visible structure (*Chardezia caudata*, *Ogdeniella lucida*), but the shells of most of them are formed by round, elliptic, or rectangular plates of organic origin, like the testa of many common freshwater testate amoebae from the order Euglyphida.

4. Presence of caudal or lateral shell spikes or protrusions (growths), preventing transport of the animals by continual water currents from land to sea or by infiltrated sea waves. Some strict psammobionts (*Alepiella tricornuta*, *Lagenidiopsis valkanovi*, and *Ogdeniella elegans*) possess lateral spikes, and many others have well-expressed caudal spikes, as in *Pseudocorythion acutum*, *Chardezia caudata*, *Micropsammella retorta*, etc. (Fig. 11).

5. Presence of a funnel-shaped or disk-like collar around the aperture, the given collar being composed of organic material and having a flexible periphery. This characteristic formation functions like a cupping-glass and fixes the animals securely on mobile sand grains in supralittoral sand sediments (Fig. 12). The majority of known psammobiotic testate amoebae possess such a characteristic formation, whose function is also related to feeding of the animals.

Among the biological adaptations of interstitial testate amoebae to their specific habitat, the following peculiarities can be singled out:

1. Tolerance to changes of salinity in the interstitial habitat. The bulk of marine interstitial testate amoebae are euryhaline and survive wide variations of salinity in the interstitial habitat – from 2-5% in some brackish seas (such as the Baltic) to 37% in tropical seas. Salinity of the underground water of sand beaches depends on many factors, for example, the regular occurrence of stormy seas, intensity of the current of continental freshwater, summer evaporation, etc.

2. Interstitial testate amoebae are bacterivorous and algivorous organisms. The cytoplasm of the animals often contains diatoms, green and brown unicellular algae, organic materials, but parasitism or rapacity have never been observed and published. They “lick” the surface of sand grains for bacteria, fungi, and algae with their pseudopodia or take food in by phagocytosis (Fig. 12).

3. Formation of cysts during periods when the habitat dries up. Some psammobiotic species (such as *Centropyxiella arenaria* and *Alepiella tricornuta*) often close the cysts by means of an organic cap (epiphragm) in the region of the aperture, but most psammobionts from the genera *Pseudocorythion*, *Corythionella*, *Cyphoderia*, *Psammobiotus*, *Pomoriella*, etc. form round cysts with a double envelope and no epiphragm (Fig. 13).

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## REFERENCES

- Adl, S. M. et al. (2005). The new higher level classification of eucaryotes with emphasis on the taxonomy of protists. *J. Eukaryot. Microbiol.* 52 (2), 399-451.

- Awerintzew, S. (1903). Beitrage zur Kenntnis der marinen Rhizopoden. *Mitt. Zool. Stat. Neapel* **16** (3), 349-364.
- Bonnet, L. (1961). Caractères généraux des populations thécamoebiens endogées. *Pedobiologia* **1** (1), 6-24.
- Bonnet, L. (1964). Le peuplement thécamoebien du sol. *Rev. Ecol. Biol. Sol* **1** (1), 123-408.
- Bonnet, L. (1975). Types morphologiques, écologie et évolution de la theque chez les thécamoebiens. *Protistologica* **2** (3), 363-378.
- Buchinski, P. H. (1895). Protozoans from the Hadzhibey and Kuyalnitski firths. *Zap. Novorossiysk. Obshechest. Estestvoispytat.* **20** (1), 137-148.
- Chardez, D. (1971). Etude sur les técamoebiens des biotopes interstitiels, psammons littoraux et zones marginales souterraines des eaux douces. *Bull. Rech. Agronom. Gembloux* **6**, (3-4): 257-268.
- Chardez, D. (1972 a). *Voluta hemispiralis*. Técamoebiens psammophile nouveau. *Rev. Verv. Hist. Nat.* **29**, 10-12.
- Chardez, D. (1972 b). Etudes sur les protozoaires psammophiles littoraux. *Ron. Anteur* 1-13.
- Chardez, D. (1977). Thécamoebiens du Mésopsammon des plages de la Mer du Nord. – *Rev. Verv. Hist. Nat.* **4/6**, 18-34.
- Chardez, D. (1978). *Hyalosphenia savoiei* sp. nov. (Técamoebiens mesopsammique). *Rev. Verv. Hist. Nat.* **7/9**, 46.
- Coineau, N. (1970). Dernières recherches sur les eaux souterraines littorales et les milieux interstitiels littoraux. *Bull. Soc. Ecol.* **1** (4), 215-222.
- Decloitre, L. (1972). Técamoebiens du Var. *Ann. Soc. Sci. Nat. Archéol. Toulon Var*, 164-177.
- Decloitre, L. (1975). Técamoebiens observé dans la zone littorale et supralittorale au Brusac à Six-Four-les Plages. *Ann. Soc. Sci. Nat. Archéol. Toulon Var*, 171-180.
- Deflandre, G. (1953). Thecamoebiens (Rhizopoda, Testacea), In: *Traite de Zoologie*, 1 (2). Masson, Paris.
- Delamare-Deboutville, C. (1960). *Biologie des Eaux Souterraines Littorales et Continentales*. Hermann, Paris.
- De Saedeleer, H. (1934). Beitrag zur Kenntnis der Rhizopoden: morphologische und systematische Untersuchungen und Klassifikationsversuch. *Mem. Mus. Roy. Hist. Nat. Belg* **60**, 1-112.
- Golemansky, V. (1969). Sur une biocenose thécamoebienne peu connue des eaux souterraines littorales des mers, In: *Progress in Protozoology*, III, 194. Nauka, Leningrad.
- Golemansky, V. (1970a). Rhizopodes nouveaux du psammon littoral de la Mer Noire. *Protistologica* (Paris) **6**, (4), 365-371.
- Golemansky, V. (1970b). *Psammonobiotus communis* Golemansky, 1968 (Rhizopoda: Testacea) - une relicte marine du lac d'Ohrid. *Bull. Inst. Zool. Mus. Sofia* **32**: 3-68.
- Golemansky, V. (1970c). Contribution a la connaissance de técamoebiens (Rhizopoda: Testacea) des eaux souterraines littorales du golf de Gdansk (Pologne). *Bull. Inst. Zool. Mus. Sofia* **32**: 77-87.
- Golemansky, V. (1970d). *Chardezia caudata* gen. n. sp. n. et *Rhumbleriella filosa* gen. n. sp. n. - deux técamoebiens nouveaux du psammon littoral de la Mer Noire (Rhizopoda: Testacea). *Bull. Inst. Zool. Mus. Sofia* **32**: 121-125.
- Golemansky, V. (1970e). Técamoebiens (Rhizopoda: Testacea) des eaux souterraines de quelques plages de Cuba. *Bull. Inst. Zool. Mus. Sofia* **32**, 151-158.
- Golemansky, V. (1974a). **Psammonobiotidae fam. nova - une nouvelle famille de thécamoebiens** (Rhizopoda: Testacea) du psammal supralittoral des mers. *Acta Protozool.* **13**, (2), 137-141.
- Golemansky, V. (1978). Adaptations morphologiques des thécamoebiens psammobiontes du psammal supralittoral des mers. *Acta Protozool.* **17**, (1), 141-152.
- Golemansky, V. (1980). *La Faune Thécamoebienne Interstitielle du Psammal Supralittoral des Mers*, 446 pp. PhD Thesis, Institute of Zoology, Bulgarian Academy of Sciences.

- Golemansky, V. (1986). Thécamoebiens (Rhizopoda: Testacea), In: *Stygofauna Mundi*, 5-16. Brill, Leiden.
- Golemansky, V. (1990). Interstitial testate amoebas (Rhizopoda: Testacea) from the Mediterranean basin. *Stygologia* **5** (1), 49-54.
- Golemansky, V., and M. M. Couîteaux (1982). Etude en microscopie électronique à balayage de huit espèces de thécamoebiens interstitiels du supralittoral marin. *Protistologica (Paris)* **18**, (4): 473-480.
- Golemansky, V., and M. Todorov (2004). Shell morphology, biometry, and distribution of some marine interstitial testate amoebae (Sarcodina: Rhizopoda). *Acta Protozool.* **43**: 147-162.
- Golemansky, V., and M. Todorov (2006). New data on shell ultrastructure and biometry of the marine interstitial testate amoebae (Rhizopoda: Testacea). *Acta Protozool.* **45**, 301-312.
- Gruber, A. (1884). Die Protozoen des Hafens von Genua. *Nova Acta Ksl. Leop.-Carol. Deut. Akad. Naturforsch.* **46** (4), 475-539.
- Laminger, H. (1973). Notes on some Testacea (Protozoa, Rhizopoda) of the Yugoslavian Coast of the Adriatic near Rab. *Hydrobiologia* **42** (1), 153-154.
- Levine, N. D. (1980). A newly revised classification of the Protozoa. *J. Protozool.* **7** (1), 37-58.
- Meisterfeld, R. (2000). Order Arcellinida Kent, 1880, In: *An Illustrated Guide to the Protozoa* (Eds. J. J. Lee, G. F. Leedale, and P. Bradbury), Second Edition, Vol. 2, 828-854. Society of Protozoologists, Lawrence, Kansas.
- Möbius, K. (1889). Bruchstücke einer Rhizopodenfauna der Kieler Bucht. *Abhandl. Königl. Preuss. Akad. Wiss. Berlin vom Jahre 1888*, 1-31.
- Ogden, C. G., and M.-M. Couîteaux (1989). Interstitial marine rhizopods (Protozoa) from the littoral sands of the East Coast of England. *Europ. J. Protistol.* **24**, 281-290.
- Page, F. C. (1976). An Illustrated Key to Freshwater and Soil Amoebae. *Freshwater Biol. Assoc. Sci. Publ.* **34**, 1-155.
- Peres, J.-M., and J. Picard (1958). Manuel et bionomie benthique de la Méditerranée. *Rec. Trav. Stat. Mar. Endoume* **23**, 7-123.
- Schonborn, W. (1964). Lebensformtypen und Lebensraumwechsel der Testaceen. *Limnologica* **2** (3), 321-335.
- Schonborn, W. (1999). *Einheitliche Theorie von Ökosystem und Phylogenie*. Shaker Verlag, Aachen.
- Schulze, F. E. (1874). Rhizopodenstudien. III. *Arch. Mikr. Anat.* **11** (1), 94-139.
- Sudzuki, M. (1977a). Protozoans in marine beach interstices. II. Taxonomy and ecology of Testacea from a sandy island recently constructed. *Jap. J. Protozool.* **8**, 23.
- Sudzuki, M. (1977b). Recent portraits of wild biota of Japan. III. A man-made sandy beach constructed in the Bay of Tokyo. *Öbun Ronsó* **8**, 221-239.
- Sudzuki, M. (1979). Psammobiont Rhizopoda and Actinopoda from marine beaches of Japan. *Acta Protozool.* **18**, (2): 239-304.
- Swedmark, B. (1964). The interstitial fauna of marine sand. *Biol. Rev. Cambridge Philos. Soc.* **1**, 1-42.
- Thomas, R. (1959). Les thecamoebiens muscicoles et terricoles: notion d'écologie générale et comparative. *P.V. Soc. Linn. Bordeaux* **99**, 1-27.
- Valkanov, A. (1954). Beitrag zur Kenntnis unsere Schwarzmeerfauna. *Trav. Stat. Biol. Marine Varna* **18**, 49-53.
- Valkanov, A. (1970). Beitrag zur Kenntnis der Protozoen des Schwarzen Meeres. *Zool. Anz.* **184** (3/4), 241-290.
- Wailes, G. H. (1927). Rhizopoda and Heliozoa from British Columbia. *Ann. Mag. Nat. Hist.* **20** (Ser. 9), 153-156.
- Zassouchin, D. N. (1931). Lebensbedingungen der Mikrofauna in Sandausschwemmungen der Flüsse und im Triebsand der Wüsten. *Arch. Hydrobiol.* **22**, 369-388.