

A checklist of Amoebozoa species from marine and brackish-water biotopes with notes on taxonomy, species concept and distribution patterns

Alexander Kudryavtsev¹, Ekaterina Volkova¹ and
Fyodor Voytinsky^{1,2}

¹ *Laboratory of Cellular and Molecular Protistology, Zoological Institute of the Russian Academy of Sciences, 199034 Saint Petersburg, Russia*

² *Department of Invertebrate Zoology, Faculty of Biology, Saint-Petersburg State University, 199034 Saint Petersburg, Russia*

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Summary

The aim of the present review is to bring together the main references on the diversity of species, geographic distribution, taxonomy, and phylogeny of naked Amoebozoa from marine and brackish water environments, including those directly connected with the World Ocean, as well as continental saline biotopes. The main body of data is structured in the tables according to the most recent classification of Amoebozoa, which list all published species names with references to the initial descriptions, redescrptions where applicable, data on the biotopes where the species were found, available strains, salinity tolerance ranges, and types of available published data including light and electron microscopical studies, and Genbank accession numbers of published sequences. In addition, we provide a brief overview of the history of investigations of marine amoebae, briefly discuss the current state of their species concept, and current knowledge of their relations to environmental salinity.

Key words: amoebae, biodiversity, biogeography, marine biotopes, salinity, species problem, taxonomy

Introduction

Since publication of F.C. Page's (1983) key titled "Marine Gymnamoebae", a lot of changes have been introduced into the taxonomy of the amoeboid protists. These changes included both, additions to the number and diversity of the known species, and taxonomic rearrangements of the existing species based on the molecular phylogenetic analysis. Compared to the earlier morphology-based systems

(e.g. Jahn et al., 1974; Page, 1976a, 1987), currently used classifications are based on the combination of molecular and morphological data (Cavalier-Smith et al., 2004, 2015, 2016; Smirnov et al., 2005, 2011; Kang et al., 2017; Adl et al. 2019). The higher-level taxa in these new systems significantly differ in composition and names from the traditional groups of the earlier morphology-based systems. Moreover, some species names introduced by earlier researchers easily go overlooked and forgotten in subsequent

revisions, with the obvious risk of getting the same species described more than once under different names. This causes the need for further laborious reinvestigations and decisions of whether the taxon isolated later is the same morphospecies as described years ago, or still demonstrates enough differences that justify its description under a different name. This should often be performed in the case when no “type culture” or otherwise preserved material is available for reinvestigation and comparison. To permit easier solution of these problems, a list of published species names, preferably tracing changes in synonymy and providing literature references has to be published sometimes, providing a reference bibliographic material for biodiversity studies. We provide this list for marine and brackish water naked Amoebozoa, including, besides literature references, also data on recorded habitats where available. Within the frames of this paper, we consider all species observed in either open sea, or coastal habitats directly connected to the ocean, regardless of the salinity of a habitat (i.e. also brackish water, estuarine habitats). Species recorded in continental saline and brackish waters (saline lakes, rivers, etc., not directly connected to the ocean) are also included, as they may often include the same morphospecies as those inhabiting marine biotopes. The classification system used in this paper is basically that of Adl et al. (2019), as this system is the most up to date. The macrotaxa suggested in this system take into account the results of the most recent phylogenomic studies. At the same time it is detailed enough, listing taxa down to the level of genera. Genera proposed after the publication of this system are indicated in appropriate sections.

Brief historical overview of investigations on marine Amoebozoa

Marine amoeboid protists were most probably first mentioned by Dujardin (1841) who described and depicted several species from Mediterranean habitats. Several works describing a number of species of marine amoebae were also published in the second half of the 19th – beginning of 20th centuries (e.g. Grassi, 1881; Mereschkowsky, 1879; Gruber, 1882a, 1882b, 1883a, 1883b, 1885, 1887–1888; Frenzel, 1897; Calkins, 1902;), however, these papers were scattered over the literature and usually contained descriptions of just a few species. Some-times a lot of details on morphology and biology of the studied species were provided (e.g.

Schaudinn, 1896; Janicki, 1912), however, not much of the species diversity was described during 19th and the first quarter of the 20th century. There were no large and impactful monographs like those on freshwater amoebae by Cash and Hopkinson (1905, 1909), Leidy (1879), or Penard (1902).

The first significant monograph that contained a large number of species of marine origin was published by Schaeffer (1926). The same work set the basic principles of classification and identification of the naked amoebae in general. The number of studies started to grow later, mostly in the 1960s and 1970s. These studies in many cases represented descriptions of naked amoebae as part of the general investigation of microfauna in particular habitats (e.g. Biernacka, 1963 on the fauna of the Bay of Gdansk, or Kufferath, 1952 on the North Sea fauna near Ostende). Several studies specifically addressed the diversity of naked lobose amoebae in particular locations and included descriptions of numerous new species and genera. Among these, papers by Sawyer (1971a, 1971b, 1975a, 1975b, 1975c, 1980) should first be mentioned. Although based on only light microscopy, these studies introduced a lot of new species and several new genera. The validity of some of them was later verified using electron microscopy and molecular phylogeny (Page, 1979b; Smirnov, 1996; Peglar et al., 2003; Kudryavtsev et al., 2011, 2020). In parallel with the cited works, Page (1970a, 1970b, 1971a, 1971b, 1972a, 1972b, 1973, 1974, 1976c, 1979a, 1979b, 1980a, 1980b, 1980c, 1981a, 1981b, 1983a; Page and Willumsen, 1983) performed a significant amount of work on isolation and investigation of marine and estuarine naked lobose amoebae from the habitats in the United States (Atlantic coast) and coastal habitats of Great Britain. At the same time, some of the material he has been working on originated from the Persian Gulf and Australia (Page, 1980a, 1981b, 1983a). A detailed comparison of the diversity of species found in American Atlantic and British habitats allowed Page (1976c) to evaluate occurrence of certain species on both sides of the Atlantic Ocean. In particular, five marine/brackish water species were mentioned in this paper as present on both sides of the Atlantic.

Accumulation of species descriptions by 1979 allowed Bovee and Sawyer (1979) a publication of a key to marine and freshwater species of amoebae within the series of “Marine flora and fauna of the northeastern United States”. Four years later, Page (1983a) published a key titled “Marine Gymnamoebae” that contained a comprehensive set of light

and electron micrographs of a number of species that were mostly collected and described by the author himself. Although this key contains data on the majority of genera and species known by that time, some names, especially those from earlier works were mentioned only briefly, and some were just listed without any further data.

In parallel to the above-cited works, the papers by Karl Grell should be mentioned that contained a number of descriptions of various species of branching and plasmodial amoeboid organisms (Grell, 1966, 1988, 1991; Benwitz and Grell, 1971a, 1971b; Grell and Benwitz, 1978). The genera *Corallomyxa* and *Stereomyxa* established in these works are still included in Amoebozoa as valid taxa, although their current position is incertae sedis (Adl et al., 2019). In addition, Grell's investigations of *Paramoeba eilhardi* Schaudinn, 1896, and especially its ultrastructure (Grell, 1961; Grell and Benwitz, 1966, 1970) have set the basis for our modern understanding of this species and the whole group of marine members of Paramoebidae containing an intracellular symbiont *Perkinsela amoebae* or *Perkinsela amoebae*-like organism (PLO). Grell (1961) was the first to suggest that the "Nebenkörper" ("secondary nucleus") described in *P. eilhardi* by Schaudinn (1896) was indeed an intracellular symbiont. This hypothesis was further developed and proven in subsequent works (Grell and Benwitz, 1970; Perkins and Castagna, 1971) and ended up with the inclusion of the symbiont in Kinetoplastida by Hollande (1980) confirmed later with molecular data. Grell's strain of *Paramoeba eilhardi* became the one on which the modern understanding of this species is based, as it was deposited in the Culture Collection of Algae and Protozoa (strain CCAP 1560/2) and further investigated using molecular methods (Mullen et al., 2005; Volkova et al., 2019; Kudryavtsev et al., 2011).

Another set of studies on the diversity of marine amoebae from 1970ies-1990ies that has to be mentioned separately was the research by British and American authors including O. Roger Anderson and Andrew Rogerson. In these works, a number of species of marine and estuarine naked amoebae were described or reinvestigated (Rogerson, 1993; Anderson et al., 1997, 2003; Rogerson et al., 1998; Hauer et al., 2001,) and in addition, a number of studies on ecology of marine amoebae, including their distribution in different biotopes, abundances and relations to different environmental factors were performed (Rogerson, 1991; Rogerson and Laybourn-Parry, 1992; Anderson and Rogerson, 1995; Rogerson et al., 1996; Butler and Rogerson,

1996, 1997; Rogerson and Gwaltney, 2000). This is also important that these authors led systematic research using light and electron microscopy on Amoebozoa isolated from the inland salt-water bodies and their salinity tolerance (Rogerson and Hauer, 2002; Hauer and Rogerson, 2005a, 2005b).

The research on biodiversity of marine and brackish-water Amoebozoa continued over the second half of the 1990s into the 21st century with several papers led by Alexey Smirnov (Smirnov, 1996, 1997, 1999a, 1999b, 2001; Smirnov and Kudryavtsev, 2005) that employed a set of "classical" methods (i. e. light and electron microscopy). At the same time, an approach to Amoebozoa biodiversity investigations using molecular tools started to develop. At this stage, culture collections assembled during the previous studies (e.g. American Type Culture Collection in the United States and Culture Collection of Algae and Protozoa in the UK) became of pivotal importance. While officially these cultures were never designated as "type material" in the sense of the ICZN (historically regulating the nomenclature of heterotrophic protists including amoebae), they served as DNA sources for already described species on the eve of the molecular studies and facilitated getting their sequences without the need of reisolation and redoing the full investigation to identify a strain.

This way the first investigations of molecular phylogeny of Amoebozoa were performed (Sims et al., 1999; Amaral Zettler et al., 2000; Bolivar et al., 2001; Fahrni et al., 2003; Peglar et al., 2003; Mullen et al., 2005). These studies led to an establishment of the new system of Amoebozoa combining structural and molecular characters (Cavalier-Smith et al., 2004; Smirnov et al., 2005, 2011). Furthermore, in fact, a new standard of taxonomic studies was set with the need to combine morphological and molecular evidence in the descriptions of new taxa as well as taxonomic revisions (e.g. Smirnov et al., 2002, 2007, 2017; Dyková et al., 2005a, 2008a, 2011; Kudryavtsev et al., 2011a, 2011b, 2014, 2018, 2019, 2021; Kudryavtsev and Pawlowski, 2013, 2015; Volkova and Kudryavtsev, 2017; Kudryavtsev and Volkova, 2018, 2020; Volkova et al., 2019; Lotonin and Smirnov, 2020; Udalov et al., 2020a, 2020b). The majority of these and many other works published during this period included strains of Amoebozoa of marine, brackish and freshwater origin. Molecular taxonomy further developed into phylogenomic studies (Cavalier-Smith et al., 2015, 2016; Kang et al., 2017; Tekle et al., 2016; Tekle and Wood, 2017) that led to an emendation and

creation of the current system of Amoebozoa (Adl et al., 2019).

Another line of development of the amoebae molecular studies included attempts to elaborate DNA-barcoding tools for species identification, refinement of the species concept in Amoebozoa and setting the basis for the metabarcoding approach to detect amoebae in the natural communities. This started first with attempts to evaluate the usefulness of 18S rRNA gene for this purpose (Sims et al., 2002; Smirnov et al., 2002), continued with ITS-5.8S locus (Caraguel et al., 2007; Dyková et al., 2005), and further, with attempts to apply a standard animal DNA barcode (Hebert et al., 2003), partial sequence of mitochondrial cytochrome C oxidase subunit 1 (Cox1) gene, as a barcode for amoebae (e.g. Nasonova et al., 2010; Pawlowski et al., 2012; Tekle, 2014; Geisen et al., 2014; Zlatogursky et al., 2016). Further development of the research on this topic goes in the direction of finding and evaluating the Amoebozoa-specific barcodes, the markers derived within Amoebozoa with low degree of paralogy and enough variability to be able to discriminate between species (Bondarenko et al., 2017; Tekle and Wood, 2018).

The last direction of research on marine Amoebozoa that deserves to be mentioned here separately, is the investigations of marine amoebae that host a kinetoplastid symbiont within their cytoplasm named *Perkinsella amoebae* (Hollande, 1980) or *Perkinsella amoebae*-like organism (PLO, Dyková et al., 2008b). Three genera – *Paramoeba* Schaudinn, 1896, *Neoparamoeba* Page, 1987, and *Janickina* Chatton, 1953 – belong to this group that in the current system is member of the Dactylopodida (Adl et al., 2019), and the monophyly of this clade has been recently confirmed with molecular data (Volkova and Kudryavtsev, 2021). A specific interest in this group of marine taxa has developed as their members were frequently reported as parasites of marine invertebrates. The very first case of this parasitism (in species later included in the genus *Janickina*) was reported with the discovery of this group as parasites of Chaetognatha (Grassi, 1880), and later more hosts for these amoebae were identified, such as blue crab *Callinectes sapidus* (Sprague and Beckett, 1966, 1968; Sprague et al., 1969), sea urchin *Strongylocentrotus droebachiensis* (Jones, 1985; Jones and Scheibling, 1985), lobster *Homarus americanus* (Mullen et al., 2005) and various fishes, including farmed salmonids where they cause amoebic gill disease, or AGD (reviewed in Nowak and Archibald, 2018; English and Lima,

2020). A practical importance of this group caused a large number of publications on its diversity, biology and molecular phylogeny, including accumulation of a considerable number of sequence data that may be further used for understanding the biodiversity and evolution of Amoebozoa in general.

Changes in taxonomy of the naked lobose amoebae

Although many amoeba species have been described in the end of 19th and beginning of 20th centuries (e.g. Korotneff, 1879; Leidy, 1879; Penard, 1890, 1902; Schaudinn, 1896; Cash and Hopkinson, 1905, 1909), the taxonomy of this group has been remaining unstable since that time and almost until recently. The main obstacle for the construction of acceptable system was the nature of morphological characters of amoebae: mainly a dynamic body shape changing with time as the cell performs its activities. Few constant structures visible with light microscopy are the nucleus and cytoplasmic inclusions that do not show enough variability to allow construction of the system. Therefore, the tendency in the earlier systems of naked amoebae was on the one hand, to lump many different organisms under a single name allowing for artificial expansion of the limits of taxa, on the other hand, a single cell performing different types of activities during its life span, could be assigned to several different species based on the differences in shape. A classical example of this case is a so-called '*Amoeba radiosa*', a name that was first used by Dujardin (1841) and applied to a variety of floating (free-swimming) forms adopted by different species of amoebae.

Although various genera of amoebae were being established slowly, not all species were assigned to them correctly from the very beginning, i.e. the system has been generally developing from lower to higher diversity of the supraspecific taxa. It was only in 1926 that the first successful attempt to formalize the taxonomic characters used for naked lobose amoebae was made (Schaeffer, 1926). Further development of the system followed the trend set by Schaeffer. With the development of the theories describing amoeboid movement mechanisms (Mast, 1926), the cytological basis was established for further analysis and application of the characters used in the system. Therefore, a morphological classification of amoebae was developed based on the types and activities of pseudopodia and modes of movement

(Bovee and Jahn, 1965, 1966; Jahn and Bovee, 1965; Jahn et al., 1974; Bovee and Sawyer, 1979). A similar morphological approach was developed by F.C. Page that, however, in later years heavily relied on electron microscopic characters not used by Bovee and his coauthors (Goodfellow et al., 1974; Page, 1978, 1979a, 1979b, 1979c, 1980a, 1980b, 1980c, 1981a, 1981b, 1983a, 1983b, 1985; Page and Blakey, 1979; Page and Baldock, 1980; Page and Willumsen, 1980, 1983; Page and Kalinina, 1984). It was finally Page's system (Page, 1976a, 1976b, 1987, 1988, 1991) that became most widely accepted and used in practice until the beginning of the molecular systematic approach, while the general system of unicellular eukaryotes adopted in that time (Levine et al., 1980) was an attempt to integrate the systems of Page, and Bovee and Jahn. In later manuals, Page's system was mostly accepted, sometimes with further modifications. For example, Rogerson and Patterson (2002) grouped all naked lobose amoebae into three orders. Two of them (Euamoebida and Leptomyxida) were those used by Page, while the third one (order Centramoebida) was introduced by these authors to accommodate families Acanthamoebidae and Stereomyxidae, and it has been in use until now, although its composition changed (Adl et al., 2019).

The development of molecular phylogeny of lobose amoebae started with single-gene trees based on the small-subunit (SSU) rRNA gene analyses (Bolivar et al., 2001; Peglar et al., 2003) followed by a simultaneous analyses of SSU rRNA and actin (Fahrni et al., 2003) with the further transition to the multigene analysis based mainly on the transcriptomic and, where available, genomic data (Cavalier-Smith et al., 2015, 2016; Kang et al., 2017; Tekle and Wood, 2017). Attempts to integrate molecular data with morphological analysis led to a creation of the modern classification of Amoebozoa (Cavalier-Smith et al., 2004; Smirnov et al., 2005, 2011) that was later incorporated into the global classification of eukaryotes (Adl et al., 2019).

Among the persisting taxonomic problems of Amoebozoa is the lack of apomorphies for some clades that consistently appear in the trees, and poor support for several deep nodes. Yet, the current consensus system seems to be reasonably established; its synopsis for the clades including marine and brackish water species down to the genus level is provided in Table 1. Essentially this system uses the results of the phylogenomic study by Kang et al. (2017) including partly the taxa names proposed by Smirnov et al. (2011), and Cavalier-

Smith et al. (2016). By contrast to the earlier classifications, this system has no formal taxonomic ranges, therefore it has the potential of expansion to as many hierarchical levels as needed, when new phylogenetic lineages are introduced. At the same time this system may look "flat" in comparison to the previous ones, as no intermediary hierarchical levels are introduced for some monotypic clades.

Notes on species concept and species problem in amoebae

Data on biodiversity accumulated during the previous periods of investigation and presented in the supplementary tables essentially relied on the application of the species concept and understanding of what a species is, and how to define its borders. This fundamental biological problem is especially important for protists as these organisms are (a) frequently microscopic and sometimes poor in morphological characters that show very inconsistent patterns of variation among lineages; (b) often agamous or have "hidden" sexual processes that are not necessarily coupled to reproduction, which means a reproductive species criterion is non-applicable in most cases; (c) for the majority of taxa data on geographic distribution and ecological preferences are missing. All these problems cause the inability to produce a single, consistent species concept for all protists (reviewed in Boenigk et al., 2011). The mentioned problems are especially significant for amoeboid protists including Amoebozoa, as the majority of taxa in this group demonstrate a changeable cell shape without any permanent external structures, therefore, very few morphological characters were available for the researchers before the introduction of electron microscopy and molecular methods. In fact, for most of amoeba species established before the first quarter of the 20th century, the morphology was usually described in a very inconsistent way. While the descriptions were often very detailed and precise, the sets of characters that the researchers paid attention to varied significantly depending on the condition of cells and their physiological states. Moreover, justifications of identification by comparison of the recorded characters with previous publications were performed in very few cases, while many authors just applied either previously published names, or claimed that the studied species were not similar to any described before, and therefore deserved a new name.

Table 1. An adaptation of the current classification of Amoebozoa (Adl et al., 2019). Only clades comprising currently known naked marine/brackish water species are shown.

Amoebozoa	
Tubulinea	
Corycida (<i>Trichosphaerium</i>)	
Elardia	
Leptomyxida (<i>Flabellula</i> , <i>Rhizamoeba</i>)	
Euamoebida (<i>Amoeba</i> , <i>Hartmannella</i> , <i>Metachaos</i> , <i>Nolandella</i> , <i>Saccamoeba</i> , <i>Trichamoeba</i>)	
Evosea	
Variosea	
Flamellidae (<i>Flamella</i>)	
Holomastigida (<i>Multicilia</i>)	
Eumycetozoa	
Myxogastria	
Columellidia (<i>Didymium</i>)	
Cutosea (<i>Armaparvus</i> , <i>Sapocribrum</i> , <i>Squamamoeba</i>)	
Archamoebae	
Mastigamoebida (<i>Mastigamoeba</i>)	
Pelobiontida (<i>Mastigella</i>)	
Discosea	
Flabellinia	
Thecamoebida (<i>Thecamoeba</i>)	
Dermamoebida (<i>Mayorella</i>)	
Dactylopodida (<i>Cunea</i> , <i>Janickina</i> , <i>Korotnevella</i> , <i>Neoparamoeba</i> , <i>Paramoeba</i> , <i>Pseudoparamoeba</i> , <i>Vexillifera</i>)	
Vannellida (<i>Clydonella</i> , <i>Lingulamoeba</i> , <i>Vannella</i>)	
Stygamoebida (<i>Stygamoeba</i> , <i>Vermistella</i>)	
Centramoebia	
Acanthopodida (<i>Acanthamoeba</i> , <i>Protacanthamoeba</i>)	
Pellitida (<i>Pellita</i>)	
Himatismenida (<i>Cochliopodium</i> , <i>Ovalopodium</i> , <i>Parvamoeba</i> , <i>Planopodium</i>)	
Incertae sedis Amoebozoa (<i>Belonocystis</i> , <i>Boveella</i> , <i>Corallomyxa</i> , <i>Gibbodiscus</i> , <i>Rhabdamoeba</i> , <i>Stereomyxa</i> , <i>Striolatus</i> , <i>Triaenamoeba</i> , <i>Unda</i>)	

In fact, a similar approach was in most cases used by Schaeffer (1926) who did not discuss a degree of divergence of his 39 new species from the previously described ones, but he established the characters on which the morphological description of an amoeba species should be based. In particular, characters of the locomotive form set as a standard for species description allowed to overcome the problem of lack of permanent cell shape and get a significant amount of data from light microscopic observations. Further addition of nuclear division patterns and electron microscopy led to elaboration of a morphological species concept defined by F.C. Page for practical reason of identification as follows: “a subgroup of a genus sharing characters which make it identifiable and indicate that its members (strains, populations) are significantly more similar to each other than to other subgroups” (Page, 1988, p. 5). In practice, all possible structural characters

could be found useful to distinguish morphospecies of amoebae. Apart from the locomotive form, these could be floating forms, nuclear structure, cyst structure, and cell coat ultrastructure (reviewed in Smirnov and Brown, 2004). At the same time, in the lack of sequencing techniques, biochemical and physiological characters were not considered widely applicable for identification from the practical point of view (Page, 1988).

The body of data on taxonomy and identification of naked lobose amoebae grew based on this approach throughout the 20th century as shown in the previous section. In particular, the morphospecies concept allowed a re-isolation and identification of different species from remote habitats and over long time spans (e.g. Bovee, 1965; Page, 1979a, 1979b; Kudryavtsev, 1999, 2000; Smirnov, 1999a). This approach even allowed Page (1976c) to perform a comparison of the species composition from habitats

in Great Britain and Atlantic coast of the United States and identify at least five common marine species from both regions.

Development of DNA sequencing as a tool for systematics of amoebae in the beginning of the 21st century has made a picture of the species diversity and species structure much more complex. On the one hand, sequencing (including a DNA barcoding approach; Hebert, 2003) should allow a more precise and clear definition of the borders between species (initiated by Nassonova et al., 2010). It was expected that getting the sequence data from the independently isolated morphologically identical strains of amoebae and their comparison with sequence data from related morphologically different strains, would allow setting a threshold in the genetic distance between sequences to enable a distinction between species by comparison of their sequences (Nassonova et al., 2010). In reality, after getting a representative set of molecular (initially SSU rRNA gene) data from a number of related species, e.g. of the genus *Vannella*, it became clear that the patterns of variation between sequence data do not match the patterns of morphological variation between morphospecies (Smirnov et al., 2007). In some cases clearly different morphospecies demonstrated almost identical SSU rRNA genes. A similar situation occurred later in the genus *Cochliopodium* where the morphospecies concept was seemingly clearly set due to the presence of ultrastructurally complex scales on the plasma membrane surface (Bark, 1973). In spite of this, sequence data analysis revealed molecular identity between different morphospecies defined on the basis of a scale structure and initially designated with different names (Geisen et al., 2014; Tekle, 2014; Tekle and Wood, 2018; Kudryavtsev et al., 2021). Moreover, a considerable variability of the SSU rRNA gene even within a clonal culture (usually explained by intragenomic variability; Zlatogursky et al., 2016; Kudryavtsev and Gladkikh, 2017) makes it difficult to apply this marker alone for distinction of species. On the other hand, in the molecular studies of *Paramoeba* and *Neoparamoeba* multiple SSU rRNA gene sequences with differences in up to 53 base pairs per ca. 2000 are assigned to the same species name *Neoparamoeba pemaquidensis* (Dyková et al., 2005b). These facts led Smirnov et al. (2007) to a statement that “In the absence of knowledge about amoeba sexuality and applicability or otherwise of the biological species concept, defining amoeba species is at present a matter of convenience. Our

experience here indicates that a combination of microscopic and sequence data is more powerful than either alone, but it remains a matter of opinion just where to place species boundaries.” (Smirnov et al., 2007, p. 308).

The described problems initiated attempts to elaborate the barcoding approach to identification of amoebae and find an appropriate molecular marker for this purpose. So far, a subunit 1 of mitochondrial cytochrome c oxidase gene (Cox1) was found to be the best candidate barcode for several genera like *Vannella* (Nassonova et al., 2010), *Korotnevela* (Zlatogursky et al., 2016), and *Cochliopodium* (Geisen et al., 2014; Tekle, 2014), however, a reference database of this marker and its practical application for species identification are still at their infancy. Only few genera of naked Amoebozoa are represented by multiple species in the reference Cox1 databases. The only clades of amoebae where all known genera have their Cox1 sequences available are Dactylopodida (Kudryavtsev and Pawlowski, 2015; Zlatogursky et al., 2016; Kudryavtsev et al., 2018, 2020; English et al., 2019; Udalov et al., 2019, 2020; Volkova et al., 2019; Kudryavtsev and Volkova, 2020) and Himatismenida (Kudryavtsev, 2012; Tekle, 2014; Kudryavtsev et al., 2021). Members of other clades include *Vannella* and *Ripella* among vannellids (Nassonova et al., 2010; Kudryavtsev and Gladkikh, 2017; Kudryavtsev et al., 2019) and several genera of Tubulinea (*Copromyxa* and *Saccamoeba*; Kostka et al., 2017). Reference data for other clades are still largely missing. Two problems currently prevent an accumulation of reference data on this perspective DNA barcode. One of them is the lack of universal primers that would reliably amplify this marker in all or nearly all amoebozoans. The standard animal primers (Folmer et al., 1994) work well in many, but not all groups. For example, no Cox1 sequence data could be obtained for the dactylopodid genera *Paramoeba* and *Neoparamoeba* before specific primers were designed based on the mitochondrial genome sequence obtained using NGS approach (Volkova et al., 2019). Another problem is the lack of reference datasets with multiple species that make researchers believe that sequencing and analysis of the Cox1 gene in routine descriptions of new species is redundant once the SSU rRNA gene sequence is available. This approach significantly slows down the accumulation of reference sequences. Therefore, we suggest that the standard species descriptions in Amoebozoa must be accompanied with at least

attempts to amplify and sequence Cox1 gene together with a standard SSU rRNA, as this will facilitate an accumulation of a reference database for DNA barcoding.

Anyway, currently available results of the molecular analysis of diversity within morphospecies have shown an extensive cryptic diversity in amoebae. Already the first attempt to try DNA barcoding on members of the genus *Vannella* revealed multiple Cox1 gene sequences in a morphospecies *V. simplex* (Nassonova et al., 2010). Furthermore, several cryptic species were identified later among marine amoebae. For example, members of the genus *Cunea* Kudryavtsev and Pawlowski, 2015 are three independently isolated species that were found in deep-sea benthos in Atlantic Ocean, sublittoral benthos in the Red Sea, and brackish continental spring isolated from the ocean (Kudryavtsev and Pawlowski, 2015; Kudryavtsev and Volkova, 2020). All these species are identical in light and electron microscopic characters, but differ in their gene sequences, biotopes and ecological preferences, therefore are described as separate cryptic species. However, in the pre-molecular era, these strains would be easily assigned to the same nominal species that would be considered as having a broad geographical distribution. Accumulating evidence shows that the degree of cryptic speciation may be high in amoebae. Apart from the above-mentioned data, there were recently cases among *Thecamoeba* spp. (Mesentsev and Smirnov, 2019; Mesentsev et al., 2020) and *Vexillifera* spp. (Kudryavtsev et al., 2020). These data suggest that the real diversity of Amoebozoa in the natural habitats may be significantly underestimated, and calls for caution in the taxonomic conclusions on identity of the newly isolated strains with previously described species. In particular, a comparison of full datasets of new and previously described strains including available morphological and molecular data is needed for a reliable conclusion on identification. In case the type strains are lost, and not all data for comparison are available, it is highly desirable to perform re-isolation attempts from the same or at least similar biotopes as in the original descriptions of the species. As the knowledge on these biotopes and their conditions are of crucial importance for such studies, we composed an interactive map for the isolation sites of different species of marine and brackish water Amoebozoa based on the published data. This map is based on Google Maps application, and is available through the following link: <https://>

www.google.com/maps/d/u/0/edit?mid=1YG4eBSsKapFzL58s7a63KpVno24&usp=sharing for free use and editing.

Salinity: one of the key environmental factors and its influence on marine amoebae

The environmental salinity is long recognized as a key factor that influences the biology and distribution of organisms in marine environment. There are different levels of salinity (usually defined in ppt or ‰ indicating g of total salts per kg of solution; Pawłowicz, 2013) of natural water bodies on the Earth. They are usually distinguished into freshwater (below 0.5 ppt), brackish water (5–30 ppt), saline (30–50 ppt) and brine (over 50 ppt). The average salinity of the oceanic seawater is about 35 ppt. Consequently, the organisms inhabiting water bodies with different degrees of mineralization are usually classified into freshwater, brackish and marine species. Generally, the most important for the distribution and physiology of the living organisms is the concept of critical salinity and horohalinicum (Khlebovich, 1968; Khlebovich and Abramova, 2000) that is defined as the salinity range between 5 and 8 ppt where a significant shift in ionic composition of solution occurs in transition between freshwater and marine habitats (i.e. typical freshwater and marine faunas). This threshold value is important, because it serves as the border between the two faunas. A “species minimum” is considered to be a characteristic feature of the habitats with this level of salinity (Remane, 1934), although this concept is recently questioned (Telesh et al., 2011). A general analysis of the relationships between the biological communities and salinity of their environment is far beyond the scope of this review. Here, we only would like to provide a brief overview of what is known by now for marine, brackish water and hypersaline amoebae in view of their diversity, ecology and distribution in relation to salinity.

Analysis of the literature shows that in fact very little attention was paid to the relationships of marine amoebae species to environmental factors, in particular, salinity. This may be due to the fact that in most cases amoebae are difficult to observe directly in the natural samples, and can only be found by enrichment cultivation in partly artificial conditions. This means different species that grow in culture are not necessarily those that constitute an active community in a given biotope at the moment

of sampling (Smirnov, 2007), therefore data on the diversity of amoebae from a given sample isolated using given conditions do not necessarily reflect the true species diversity in a given biotope (Smirnov, 2003). Moreover, different methods are known that seemingly yield the most effective species recovery from marine biotopes using enrichment cultivation. For example, Page (1983a) recommends diluting full-strength seawater to 75% of the original to yield a higher species diversity. Yet, the question of how salinity factor limits the distribution and diversity of amoebae in the natural habitats is one of the key in biogeography of marine Amoebozoa in general.

In the most studies where this question was addressed, the range of salinity tolerance of cultured amoebae was experimentally determined. Unfortunately, until now there were no attempts to define a standard set of experimental techniques for these measurements, and the statement by Page that “The method needs further development, including quantification.” (Page, 1983a, p. 13) is valid until now. One of the pioneering studies on the influence of salinity on marine amoebae was performed by Schaeffer (1926) who reported the direct observations of the influence of diluted seawater on marine amoebae describing the immediate effect of the seawater dilution. The question remains whether the results of these experiments may be extrapolated on the long-term effect of salinity on the population of a given species and its distribution. Further experimental studies of the influence of different salinities on cell physiology were performed on *Vannella* (as *Flabellula*) *mira* (Hopkins, 1938), and an ability to tolerate different salt concentrations from ca. 1.7 to 350 ppt was determined. Later, salinity tolerance experiments on different cultures of marine and estuarine lobose amoebae were mainly performed along with their taxonomic description by Page (1971a, 1971b, 1974, 1983), Sawyer (1975a, 1975b, 1975c), Smirnov (1995, 2001; Smirnov et al., 2002), Hauer et al. (2001), Anderson et al. (2003), Kudryavtsev and Smirnov (2006), Cole et al. (2010), Kudryavtsev and Volkova (2018, 2020), and Kudryavtsev et al. (2019, 2020). Although these works provide some useful information on the salinity tolerance of certain amoeba species, the experimental methods based on inoculation of the cultures in different salinities and observations of subsequent growth are not consistent between these publications and are rather qualitative than quantitative. Therefore additional studies have to be performed to set up a really reproducible and

quantifiable method of salinity tolerance testing, as well as get a reliable dataset on the tolerance ranges of marine and brackish water amoeba species. Until now, some quantitative experiments to evaluate the growth rates of the naked amoebae cultures depending on the salinity level were performed by Hauer and Rogerson (2005a) and Cowie and Hannah (2006). The amoebae studied, were isolated from the continental and partly hypersaline Salton Sea, biotopes on the coast of Florida, and intertidal habitats in the Kames Bay (North Sea) where salinity was fluctuating.

Another approach to experimental investigations of relationships between brackish and fresh water amoebae faunas was an experiment by Smirnov (2007) that demonstrated a presence of a hidden community of freshwater amoebae in a brackish biotope. In the current state of research, this approach can be successfully coupled with sequencing of environmental DNA to get a fuller picture of the community not influenced by cultivation bias. Along with experimental research to determine how the environmental salinity limits the distribution of different species in the environment, an important point is the cell physiological mechanisms that provide an adaptation of amoebae to different salinity levels, about which virtually nothing is known yet.

To summarize a current situation in our knowledge of the salinity tolerance of various marine and brackish water amoebae, we can mention, that there are fractions of euryhaline and stenohaline species, as well as some typical freshwater species that may be isolated from brackish water biotopes (Page, 1970a; Garstecki and Arndt, 2000; Smirnov, 2007). At the same time it is believed that marine species cannot be isolated from the true freshwater environments, and this was the reason why Page (1988) established a species *Vannella cirrifera* (Frenzel, 1892) to accommodate a freshwater strain that he previously identified as *V. mira* (Schaeffer, 1926). The main reason for this was that *V. mira* was a marine species, and its isolation from a freshwater environment violated a general belief that no marine amoebae can be isolated from fresh water (Page, 1988). However, as shown later, the use of the name *V. cirrifera* was probably not justified by Page, while *V. mira* was finally correctly redescribed as a marine species with establishment of the neotype (Smirnov 2002). The ways how salinity limits the distribution areas for different species, the degrees of ecological plasticity, as well as mechanisms of adaptation to different salinity values are largely unknown for Amoebozoa.

A synopsis of the current names of marine Amoebozoa

PRELIMINARY NOTES ON THE STRUCTURE OF TABLES AND DATA PROVIDED

The tables below are intended to provide some pieces of data on currently known species of marine naked Amoebozoa from the previously published literature, and to serve as a guide and archive of this literature. We included as many previously published species names as possible, as well as designations of unnamed strains where relevant. The species names (column “Species”) are provided in their published form, under those genera where they were included most recently (i. e. in a currently accepted combination). Within the frames of this paper, we do not intend to evaluate either validity of certain genera and species or ability to recognize them in case of re-isolation. Hence, the collection of species names is intended to be as full as possible. However, the reader is strongly advised against considering all these names as valid and applicable. In particular, some of these species, especially those described only before 1960s using only light microscopy may be difficult to identify in future based on only original descriptions provided. Therefore, evaluation of diversity based on these data should be performed with caution (see also Smirnov and Brown, 2004). Comments on the composition and status of the listed genera in marine/brackish water biotopes are provided with each table.

The column “Initial description” contains references to the works where the species name appeared for the first time and that constitute a publication in the sense of ICZN. The column “Redescription(s) and earlier synonyms (if present)” provides references to the publications where the species was transferred into the genus where it is currently accommodated, and previous names under which the species were published initially. Cultured or preserved strains that are assigned to a given species are listed to the best of our knowledge under the column “Strains if available”. The following conventions are accepted in this column: “+” after strain designation indicates that the strain is lost; (T) indicates type strain (by which we mean here the strain that was used for species description, regardless of whether it was designated as “type” in the publication itself). Abbreviations of the culture collections preceding accession numbers are as follows: ATCC = American Type Culture Collection;

CC = Culture Collection of Cryopreserved Strains of the Institute of Parasitology, Biology Centre of the Academy of Sciences of the Czech Republic; CCAP = Culture Collection of Algae and Protozoa (UK); CCM = Culture Collection of Microorganisms at the Research Park of Saint-Petersburg State University (Russia); CCZ = Culture Collection of Protists of the Zoological Institute, Russian Academy of Sciences (Russia); SAUT = culture collection of the School of Aquaculture, University of Tasmania (Australia). The column “Habitat” lists the habitats where the species was found. Several different habitats may be listed with appropriate reference if more than one strain was studied (in the same or different publications). We attempted to indicate, as far as possible, the following data: biotope with environmental metadata where available and geographic location with coordinates (in the majority of cases, the coordinates had to be deduced from the descriptions of locations, hence they are indicated approximately). “Salinity tolerance range” provides limits of salinity tolerance range reported in the cited papers. We indicated where possible, whether the limits are based on growth or survival experiments. The column “Data available” cites literature containing different types of data on a species. Conventions are as follows: “LM” indicates light microscopic data available including drawings and/or micrographs; “EM” indicates electron microscopic data (transmission and/or scanning electron microscopy); “Seq” indicates single-gene sequences, besides citation, we provide names of the genes and GenBank accession numbers; “Tr” indicates accession number for available transcriptomic data, while “G” is reserved for genome sequences.

Tubulinea, Elardia, Euamoebida (Table 2).

***Amoeba* Bory de St. Vincent, 1822.** In spite of numerous descriptions, especially in the older works, no modern evidence of isolation of any species of this genus (with its modern diagnosis) from marine or brackish water habitats exist. The last brackish water organisms described as species of *Amoeba* and not subsequently transferred into other genera were isolated by Kufferath (1952). All species names provided here should either be reclassified or invalidated in future.

***Metachaos* Schaeffer, 1926.** This monotypic genus has never been re-isolated since the description by Schaeffer (1926).

Table 2. *Ttubulinea*, *Elardia*, *Euamoebida*.

Species	Initial description	Redescription and earlier synonyms (if present)	Strains if available	Habitat	Salinity tolerance range	Data available
<i>Amoeba Bory de St. Vincent, 1822.</i>						
<i>Amoeba alveolata</i>	Mereschkowsky 1879			Algal growth at the influx of a small freshwater stream, Monastery Bay, Solowetsky Archipelago, White Sea, Russia, salinity probably changeable		LM: Mereschkowsky 1879
<i>A. crassa</i>	Dujardin 1841			Mediterranean seawater (Dujardin 1841); detritus and sand, among <i>Ectocarpus</i> interstitials, Monastery Bay, Solowetsky Archipelago, White Sea, Russia (Mereschkowsky 1879)		LM: Mereschkowski 1879
<i>A. crystalligera</i>	Gruber 1885			Marine aquarium with material from the Frankfurt-am-Main Zoo (Germany)		LM: Gruber 1885
<i>A. filifera</i>	Mereschkowsky 1879			Algae, Monastery Bay, Solowetsky Archipelago, White Sea, Russia		LM: Mereschkowsky 1879
<i>A. flava</i>	Gruber 1885			Marine aquarium with material from the Frankfurt-am-Main Zoo (Germany)		LM: Gruber 1885
<i>A. flowersi</i>	Jones 1945			Great Salt Lake, Utah (US)		LM: Jones 1945
<i>A. fluida</i>	Gruber 1885			Marine aquarium with material from the Frankfurt-am-Main Zoo (Germany)		LM: Gruber 1885
<i>A. hostilis</i>	Kufferath 1952			Port of Ostende		LM: Kufferath 1952
<i>A. ('Amiba') marina</i>	Dujardin 1841			Seawater		LM: Dujardin 1841
<i>A. minuta</i>	Mereschkowsky 1879			Detritus and sand, Solowetsky Archipelago, White Sea, Russia		LM: Mereschkowsky 1879
<i>A. ostendensis</i>	Kufferath 1952			Port of Ostende		LM: Kufferath 1952
<i>A. placida</i>	Kufferath 1952			Bay of Ostende		LM: Kufferath 1952
<i>A. salinae</i>	Frenzel 1897			<i>Branchipus</i> sp. in marine aquarium		LM: Frenzel 1897
<i>Metachaos Schaeffer, 1926</i>						
<i>Metachaos fulvum</i>	Schaeffer 1926	Mentioned as <i>Saccamoeba fulvum</i> in Bovee and Sawyer 1979		Irrigated culture, seawater: Tortugas, Florida, US	3.5-35 ppt	LM: Schaeffer 1926
<i>Trichamoeba Fromentel, 1874.</i>						
<i>Trichamoeba gumia</i>	Schaeffer 1926	Mentioned as <i>Saccamoeba gumia</i> in Bovee and Sawyer 1979		Tidal pool: Cold Spring Harbor, Long Island, US	10-35 ppt	LM: Schaeffer 1926
<i>T. pallida</i>	Schaeffer 1926	Mentioned as <i>Rhizamoeba pallida</i> in Bovee and Sawyer 1979		Seawater: Tortugas, Florida, US	10-35 ppt	LM: Schaeffer 1926
<i>T. schaefferi</i>	Radir 1927			Ca. 36.61949N, 121.90333W, seawater in tidal pools associated with <i>Bunodactis</i> sp.: Monterey Bay, Pacific Grove, California (US)	17-35 ppt	LM: Radir 1927

Table 2. Continuation.

<i>T. sphaerarium</i>	Schaeffer 1926	Mentioned as <i>Rhizamoeba sphaerarium</i> in Bovee and Sawyer 1979	Seawater: Tortugas, Florida, US	26-35 ppt	LM: Schaeffer 1926
Saccamoeba Frenzel, 1892.					
<i>Saccamoeba admirata</i>	Goodkov and Buryakov 1987	This species most probably belongs to the genus <i>Trichamoeba</i> (A.V. Goodkov, pers. comm.), see table for <i>Trichamoeba</i> .	Ca. 66.337N, 33.62456E and 66.33639, 33.63872; submerged natural (macroalgae, hydroid colonies) and artificial (glass slides) substrates, Kruglaya and Levaya bays, Chupa Inlet, Kandalaksha Bay, the White Sea (Russia); 21-24 ppt.		LM: Goodkov and Buryakov 1987
<i>Saccamoeba marina</i>	Anderson et al. 1997		55.75116N, 4.91666W; sandy bottom sediments, depth ca. 10 m, Kames Bay, UK; salinity 32.4 ppt		LM, EM: Anderson et al. 1997
Hartmannella Alexeieff, 1912.					
<i>Hartmannella lobifera</i>	Smirnov 1996/97		55.92054N, 12.52338E; upper layer of sediments (sand, anaerobic bacterial mats), Nivå Bay, The Sound, Denmark		LM, EM: Smirnov 1996/97
<i>H. tahitiensis</i>	Cheng 1970		17.73524S, 149.33922W; moribund oyster (<i>Crassostrea commercialis</i>) tissues, depth 1.5-3 m, Tahiti, French Polynesia; salinity 15-18 ppt, temperature +27.4-39°C (Cheng 1970)		LM: Cheng 1970
<i>H. vacuolata</i>	Anderson et al. 1997		55.75116N, 4.91666W; sandy bottom sediments, depth ca. 10 m, Kames Bay, UK; salinity 32.4 ppt (Anderson et al. 1997)		LM, EM: Anderson et al. 1997
Nolandella Page, 1983.					
<i>Nolandella hibernica</i>	Page 1980c	Page 1983a; <i>Hartmannella hibernica</i> (Page, 1980)	Tidal pool on a sandy beach: White Strand, Lisconnor Bay, near Lahinch, County Clare, Ireland (Page 1980c)		LM, EM: Page 1980c, 1983a Seq: JQ519510 (SSU rDNA), Lahr et al. 2013
<i>N. abertawensis</i>	Page 1980c	Smirnov et al. 2011; <i>Hartmannella abertawensis</i> (Page, 1980)	CCAP 1534/9; Ca. 51.61204N, 3.95971W; sandy beach, Swansea (Abertawe) Beach, Bristol Channel, West Glamorgan, Wales (UK) Page 1980c CC JKS1: marine sand: Jeju Island, South Korea (Dyková and Kostka 2013)	CCAP 1534/9 (T); CC JKS1	LM, EM (CCAP 1534/9): Page 1980c, 1983a LM, EM (CC JKS1): Dyková and Kostka 2013 Seq: CCAP1534/9: DQ190241 (SSU rDNA), Kuiper et al. 2006; AY803764 (efl.a), Steenkamp et al. 2008, unpublished CC JKS1: JQ271707 (SSU rDNA), Dyková and Kostka 2013

Trichamoeba Fromentel, 1874. The only brackish-water species that may be classified in this genus according to its modern diagnosis, was described as *Saccamoeba admirata* Goodkov and Buryakov, 1987 (A. Goodkov, pers. comm), and is listed here under *Saccamoeba* (Table 2), because no formal transfer has been done yet. The species currently listed under *Trichamoeba* may need to be reclassified in future.

Saccamoeba Frenzel, 1892. One of the two marine species of *Saccamoeba* probably belongs to *Trichamoeba*.

Hartmannella Alexeieff, 1912. The taxonomic composition of this genus has recently been modified by the transfer of *H. cantabrigiensis* into the genus *Copromyxa* (Brown et al., 2011), and the validity of *Hartmannella* is doubtful, because some of its previous species have been reclassified based on the molecular data (Kostka et al., 2017), and others have not been sequenced. Yet, in our opinion, it does make sense to reserve this name at least for the species listed in Supplementary Table 1 until they are re-isolated and investigated.

Nolandella Page, 1983. This genus comprises exclusively marine species, and initially was placed incertae sedis in lobose amoebae (Page, 1983a), although its members were included in *Hartmannella* when described for the first time (Page, 1980c). Interestingly, even after the genus *Nolandella* was established, one of its species, *N. abertawensis*, was kept in *Hartmannella* until formal transfer (Smirnov et al., 2011), although its sequence was available five years earlier (Kuiper et al., 2006). It was molecular analysis that placed *Nolandella* in the Tubulinea first (Tekle et al., 2008).

Tubulinea, Elardia, Leptomyxida (Table 3).

Flabellula Schaeffer, 1926. This genus in its current composition comprises exclusively marine amoebae, except one soil species *Flabellula kudoii* Singh and Hanumajah, 1979 that was never reinvestigated. *Paraflabellula* Page and Willumsen, 1983 is a junior synonym of *Flabellula* abandoned by Smirnov et al. (2017). It is noteworthy that Tylm et al. (2018) identified two distinct SSU rDNA clades, both morphologically corresponding to *Flabellula*.

Rhizamoeba Page, 1972. Among three named marine species (Table 3), only one was characterized using molecular data. Several species included in *Trichamoeba* are suspected to be members of *Rhizamoeba* (Smirnov et al., 2017).

Tubulinea, Corycida (Table 4).

Trichosphaerium Schneider, 1878. This is one of the most morphologically unusual genera comprising exclusively marine Amoebozoa for which a biphasic life cycle consisting of ‘spicule-bearing’ and ‘spicule-less’ generations was described by Schaudinn (1899), but never confirmed in later works. Consequently, several junior synonyms were proposed for the spicule-less forms. These names are *Pontifex maximus* Schaeffer, 1926 later identified as a synonym of *Trichosphaerium* (Page, 1983a) and *Atrichosa algivora* established by Cavalier-Smith et al. (2016) for spicule-less ATCC strain 40318, but invalidated later (Adl et al., 2019). It is noteworthy that all available sequence data were obtained for the spicule-less strain ATCC 40318.

Evosea, Variosea, Flamellidae (Table 5).

Flamella Schaeffer, 1926. This genus mostly comprises freshwater and soil amoebozoans (Bovee, 1956a; Fishbeck and Bovee, 1993; Michel and Smirnov, 1999; Kudryavtsev et al., 2009; Shmakova et al., 2016; Walthall et al., 2016; Glotova and Smirnov, 2017), however, its only marine species is the type one (*F. magnifica* Schaeffer, 1926). This species has never been reisolated since its initial description, and only one other variosean species is known from marine biotopes.

Evosea, Variosea, Holomastigida (Table 6).

Multicilia Cienkowski, 1881. A single known species of this genus is marine, and this is the second of only two known variosean species from marine biotopes.

Evosea, Eumycetozoa, Myxogastria, Columellidia (Table 7).

Didymium Schrader, 1797. The only record of Eumycetozoa in marine biotopes is represented by this genus, and its strains isolated as endobionts of sea urchins were not identified to species (Dyková et al., 2007a).

Evosea, Cutosea (Table 8).

Cutosea comprise four monotypic genera, of which three (*Armaparvus* Schuler and Brown, 2018, *Sapocribum* Lahr et al., 2015, and *Squamamoeba* Kudryavtsev and Pawlowski, 2013) are marine. This

Table 3. Tubulinea, Elardia, Leptomyxida.

Species	Initial description	Redescription and earlier synonyms (if present)	Strains if available	Habitat	Salinity tolerance range	Data available
Flabellula Schaeffer, 1926.						
<i>Flabellula baltica</i>	Smirnov 1999		CCAP 1529/6+ TF (Fenchel 2010) CC SMA17/I, M4M/I, M9M/I, PHZ1	Strains TF and CCAP 1529/6 55.92054N, 12.52338E; anaerobic bacterial mats, Nivå Bay, The Sound, Denmark; salinity 15–20 ppt (Fenchel 2010; Smirnov 1999b; Smirnov et al. 2017). Strain SMA17/I: gill tissue, <i>Scophthalmus maximus</i> , fish farm, North-Western Spain (Dyková et al. 2008a; Smirnov et al. 2017). Strain M4M/I: Ca. 23.25097N, 106.46055W, gills of orangeside triggerfish (<i>Sufflamen verres</i>) collected off the coast of Mazatlan, Sinaloa (Mexico), Dyková et al. 2008a. Strain M9M/I: Ca. 23.25097N, 106.46055W, gills of orangeside triggerfish (<i>Balistes polylepis</i>) collected off the coast of Mazatlan, Sinaloa (Mexico), Dyková et al. 2008a. Strain PHZ1: ca. 13.75633N, 120.91855E, wet sand from beach, coast of Anllao, Luzon, (Philippines), Tymi et al. 2018		LM, EM: Dyková et al. 2008a; Fenchel 2010; Smirnov 1999b; Smirnov et al. 2017. Seq: EU852657, EU852653, (SSU rRNA), Dyková et al. 2008a; KT934049, KT945248 (SSU rDNA), Smirnov et al. 2017; LC340976 (SSU rDNA), LC340989–LC340992, LC341037–LC341039 (actin), Tymi et al. 2018
<i>Flabellula calkinsi</i>	Hogue 1914	Bovee 1965; <i>Vahikampfia calkinsi</i> (Hogue 1914)	CCAP 1529/1	Oyster digestive tract, Woods Hole, Massachusetts, US (Hogue 1914) Seawater, mud, edge of Damariscotta River, Damariscotta, Maine, US; 29–30 ppt (Page 1971a), Marine, Mersea, Essex, UK (Page 1976c)		LM: Hogue 1914, Page 1971a EM: Page 1980c
<i>F. citata</i>	Schaeffer 1926		CCAP 1529/2	Seawater, seaweeds, Tortugas, Florida, US; Cold Spring Harbor, Long Island, US; Casco Bay, Maine, US (Schaeffer 1926). Seawater, mud, Day's Cove, Damariscotta River estuary, Damariscotta, Maine, US; 29–30 ppt (Page 1971a). Marine, Brancaster, Norfolk, UK (Page 1976c)	Euryhaline (Schaeffer 1926); 3–30 ppt (Page 1971a)	LM: Schaeffer 1926; Page 1971a; Dyková et al. 2008a EM: Page 1980c Seq: EU852654 (SSU rRNA), Dyková et al. 2008a; LC340977–LC340980 (actin), Tymi et al. 2018 Tr: SAMN06642716 (Kang et al. 2017)
<i>F. demetica</i>	Page 1980c		CCAP 1529/3(T+), probably preserved in CC (Dyková and Kostka 2013)	Seawater, mud: St. Bride's Bay, Newgale, Dyfed, UK (Page 1980c)		LM, EM: Page 1980c, Dyková and Kostka 2013
<i>F. hoguae</i>	Sawyer 1975a	Redescribed as <i>Paraflabellula hoguae</i> (Page and Willumsen 1983). Reverted by Smirnov et al. 2017.	ATCC 30733 (T)	Surface seawater, Chincoteague Bay near Greenbackville, Virginia, US; 30.7 ppt (Sawyer 1975a). Ca. 43.31248S, 147.08289E, gills of cultured Salmo salar and cage net, fish farm, Huon estuary, Dover, southeast Tasmania, Australia (Wong et al. 2004; Young et al. 2007)	3–30 ppt (Sawyer 1975a)	LM: Sawyer 1975a Seq: AF293899 (SSU rDNA), Amaral Zettler et al. 2000; AY277297 (SSU rDNA), Wong et al. 2004; EF216916 (LSU rDNA), Young et al. 2007; JF694313–JF694315 (actin), Lahr et al. 2011.
<i>F. pellucida</i>	Schaeffer 1926			Seawater, blue-green algae, Key West Harbor, Florida, US (Schaeffer 1926)	Freshwater–30 ppt (Schaeffer 1926)	LM: Schaeffer 1926
<i>F. pomeranica</i>	Smirnov et al. 2017			Sand, detritus, littoral zone of a beach to the west from Kostock, The Baltic Sea, Mecklenburg-Western Pomerania, Germany; salinity 8–9 ppt (Smirnov et al. 2017)		LM, EM: Smirnov et al. 2017 Seq: KT1945249, KT1986068–KT1986072 (SSU rDNA), KT1986073–KT1986075 (actin), Smirnov et al. 2017

Table 3. Continuation.

F. reniformis	Schmoller 1964	Smirnov et al. 2017; Rugipes reniformis (Schmoller 1964); Paraflabellula reniformis (Page and Willumsen 1983)	ATCC 50741 (isolated by T.K. Sawyer, habitat unknown)	Seawater, green algae: upper littoral zone, ca. 2.5 km west from Rostock Warnemünde Pier, Baltic Sea, Germany (Schmoller 1964). Gravel, coarse silt, small pieces of green alga Ceramium rubrum, depth 8 m: Svendborg Sound, central Danish Belt Sea; 15-24 ppt (Page and Willumsen 1983)	"apparently very euryhaline" (Page 1983)	LM: Schmoller 1964 LM, EM: Page 1983a; Page and Willumsen 1983 Seq: AF293900 (SSU rDNA), Anaral Zettler et al. 2000	
F. sawyeri	Tyml et al. 2018		CC GAU17(T), GAU16, CSP3, CSP6, NETC3/1, STAR2	GAU17, GAU16: Ca. 62.00N, 7.292E; kelp (Laminaria sp.) surface, coast of Vevang, Trondheim, Norway. CSP3, CSP6: Oyster (Crassostrea sp.) mantle cavity, geographic origin unknown. NETC3: Floating cage surface, Atlantic salmon farm, Tasmania, Australia. STAR2: Ca. 62.00N, 7.292E; starfish (Porania pulvillus) stomach: coast of Vevang, Trondheim, Norway.		LM, EM: Dyková et al. 2008a; Dyková and Kostka 2013; Tyml et al. 2018 Seq: EU852656, EU852658, LC340972- LC340975 (SSU rRNA), Dyková et al. 2008a, Tyml et al. 2018; LC340984- LC340988 (actin), Tyml et al. 2018	
F. schaefferi	Tyml et al. 2018		CC RT11(T)	Ca. 9.3810N, 84.1456W; wet sand, Manuel Antonio Beach, Costa-Rica.		LM, EM: Dyková and Kostka 2013; Tyml et al. 2018 Seq: JQ271708 LC340972-LC340975 (SSU rRNA), Dyková and Kostka 2013; LC341016-LC341020 (actin), Tyml et al. 2018	
F. trinovantica	Page 1980c		CCAP 1529/4(T) CC ISO14, S3M27, S5M32, SBGL1	CCAP 1529/4: Ca. 51.7733N, 0.9182E, seawater; mud, River Blackwater estuary, West Mersea, Essex, UK (Page 1980c) ISO14, SBGL1: gills of European seabass (Dicentrarchus labrax), Sicily, Italy S3M27, S5M32: gills of turbot (Scophthalmus maximus), Galicia, Spain		LM, EM: Page 1980c; Tyml et al. 2018 Seq: JQ271682 (SSU rDNA), Dyková and Kostka 2013; LC340981 - LC340983 (actin), Tyml et al. 2018	
Flabellula sp.	Dyková et al. 2008a	Listed under Paraflabellula by Dyková and Kostka 2013	CC SEDF	Sediments, Atlantic salmon (Salmo salar) farm, Tasmania, Australia		LM, EM: Dyková et al. 2008a; Dyková and Kostka 2013; Tyml et al. 2018 Seq: EU852655 (SSU rDNA) Dyková et al. 2008a	
Flabellula sp.	Dyková and Kostka 2013, Tyml et al. 2018	Listed under "Strains incertae sedis, group 03" by Dyková and Kostka 2013	CC ROD2G ROD4G ROD5G ROD8G	Gills of turbot (Scophthalmus maximus), Galicia, Spain		LM, EM: Dyková and Kostka 2013, Tyml et al. 2018 Seq: JQ271780- JQ271783 (SSU rDNA) Dyková and Kostka 2013, LC340993- LC341015 (actin) Tyml et al. 2018	
Rhizamoeba Page, 1972.							
Rhizamoeba polyura	Page 1972a			Ca. 44.02756N, 69.52809W, mud flat, seawater, edge of Day's Cove, Damariscotta River estuary, Damariscotta, Maine, US; salinity 29-30 ppt		LM: Page 1972a	
R. saxonica	Page 1974b		CCAP 1570/2(T) ATCC 50812 (isolated by T.K. Sawyer, habitat unknown)	Ca. 51.77333N, 0.91821E, seawater, tidal pool on the West Mersea Beach on Mersea Island, Essex, UK (Page 1974b)		LM: Page 1974b; Smirnov et al. 2008 LM, EM: Page 1980c, 1983a Seq: EU719197 (SSU rDNA), Smirnov et al. 2008; GU001159 (SSU rDNA- ITS-5.8S-LSU rDNA), Glücksman et al. 2011; other sequence data available in Genbank under this name originate from the strains with unverified identity. Tr: SAMN06642736 (from ATCC 50812 strain, Kang et al. 2017)	
R. schneppii	Kühn 1996/97			55.00833N, 8.25833E; plankton collected in the German Bight off the Sylt Island, North Sea; water temperature 16-17 °C		LM: Kühn 1996/97	

Table 4. Tubulinea, Corycidea.

Species	Initial description	Redescriptions and earlier synonyms (if present)	Strains if available	Habitat	Salinity tolerance range	Data available**
Trichosphaerium Schneider, 1878.						
Trichosphaerium sieboldi	Schneider 1878	Amoeba tentaculata (Gruber 1882a, 1882b); Pachymyxa hystrix (Gruber 1883a, 1883b); Pontifex maximus (Schaeffer 1926)	CCAP 1585/2; ATCC 40318; ATCC 40319	Marine aquarium with material from the Genoa Harbor, Mediterranean Sea, Italy, and the Baltic Sea (Gruber 1882a, 1882b, 1883a, 1883b); oyster bed in Ostende, North Sea coast, Belgium (Schneider 1878); dead seagrass in the Bay of Kiel, and Spirulina versicolor in aquarium with seawater, Baltic Sea, Germany (Möbius 1888); algae, littoral to 5 m depth, Puddefjorden, Bergen, Norway (Schaudinn 1899); CCAP 1585/2: ca. 50.34796N, 4.45094W, rock pools at Hannaford Point, Cornwall, UK, ca. 52.94545N, 1.21765E, sandy beach at Sheringham, Norfolk, UK (Page 1983a); spicule-bearing form: ca. 50.34796N, 4.45094W, rock pools at Hannaford Point, Cornwall, UK (Page 1983a); ATCC 40318: 34.46808N, 120.27233W, Sargassum muticum, at rocky shores, Alegria beach, Hollister Ranch, Santa Barbara County, California, US (Poline-Fuller, 1987) Spicule-less form: ca. 43.69564N, 69.99494W; seawater and Fucus sp. material, Casco Bay, Maine, US (Schaeffer 1926)		LM spicule-less form: Gruber 1882a, 1882b; Schaeffer 1926; Page 1983a LM spicule-bearing form: Gruber 1883a, 1883b; Schneider 1878; Möbius 1888 LM both forms: Schaudinn 1899; Sheehan and Banner 1973 (as Trichosphaerium sp.) EM both forms: Sheehan and Banner 1973 LM, EM spicule-bearing form: Schuster 1976 (as Trichosphaerium sp.) LM, EM spicule-less form: Poline-Fuller 1987 Seq: EU273464- EU273465, EU273471 (SSU rDNA), EU273469 (alpha-tubulin), EU273470 (beta-tubulin), Tekle et al. 2008; HQ834954 (rpb1) Tr: SAMN02740470 (Keeling et al. 2014)
T. micrum	Angell 1975			Seawater and algae: Big Pine Key and Alligator Harbor, Florida, US; Pacific Grove and Tomales Bay, California, US; ca. 18.21695S, 177.72834E, Korolevu Beach, Fiji; ca. 14.67975S, 145.45922E, Lizard Island, Great Barrier Reef, Australia; ca. 23.44303S, 151.91249E, Heron Island, Great Barrier Reef, Australia		LM, EM: Angell 1975
T. platyxyrum	Angell 1976			Seawater and algae: Big Pine Key, Florida, US; ca. 14.67975S, 145.45922E, Lizard Island, Great Barrier Reef, Australia; ca. 23.44303S, 151.91249E; Heron Island, Great Barrier Reef, Australia		LM, EM: Angell 1976

Table 5. Evosea, Variosea, Flamellidae

Species	Initial description	Redescription and earlier synonyms (if present)	Strains if available	Habitat	Salinity tolerance range	Data available
Flamella Schaeffer, 1926.						
Flamella magnifica	Schaeffer 1926			Marine blue-green algae: ca. 24.63202N, 82.92158W, Tortugas; ca. 24.56429N, 81.72625W, Key West (US)	Freshwater-30 ppt survival	LM: Schaeffer 1926

Table 6. *Evosea*, *Variosea*, *Holomastigida*.

Species	Initial description	Redescription and earlier synonyms (if present)	Strains if available	Habitat	Salinity tolerance range	Data available
Multicilia Cienkowski, 1881.						
<i>Multicilia marina</i>	Cienkowski 1881			Ca. 44.82049N, 34.90473E; washings of brown algae at 1 m depth between Novy Svet and Vesylloe settlements (Crimean Peninsula, Black Sea); salinity 18 ppt (Mikrjukov and Mylnikov 1998)	Grew in 35 ppt (Mikrjukov and Mylnikov 1998)	LM: Cienkowski 1881, Mikrjukov and Mylnikov 1998 EM: Mikrjukov and Mylnikov 1998 Seq: AY268037 (SSU rDNA) Nikolaev et al. 2006

Table 7. *Evosea*, *Eumycetozoa*, *Myxogastria*, *Columellidia*.

Species	Initial description	Redescription and earlier synonyms (if present)	Strains if available	Habitat	Salinity tolerance range	Data available
Didymium Schrader, 1797.						
<i>Didymium</i> sp.	Dyková et al. 2007a		CC: ECH1, ECH14, ECH43, ECH 49, ECH54	Coelomic fluid of sea urchins <i>Sphaerechinus granularis</i> (Lamarck, 1816), off the Brač Island (Adriatic Sea, Croatia)		LM, EM: Dyková et al. 2007a; Dyková and Kostka 2013 Seq: EF118757-EF118761 (SSU rDNA) Dyková et al. 2007a

Table 8. Evosea, Cutosea.

Species	Initial description	Redescription and earlier synonyms (if present)	Strains if available	Habitat	Salinity tolerance range	Data available
Armaparvus Schuler and Brown, 2018.						
Armaparvus languidus	Schuler and Brown 2018		ATCC PRA-29(T)	Marine invertebrate, Connecticut, US (data from https://www.atcc.org/products/prs-29 , no other data seem to be available)		LM: Tekle et al. 2008 LM, EM: Schuler and Brown 2018 Seq: EU273458 (SSU rDNA) EU273457 (actin) Tekle et al. 2008; Tr: SAMEA7820257 (Keeling et al. 2014)
Sapocribrum Lahr et al., 2015.						
Sapocribrum chincoteaguense	Lahr et al. 2015		ATCC 50979(T)	Moist soil from mud flat ca. 730 m from the ocean, Chincoteague (Virginia, US)		LM, EM: Lahr et al. 2015 Seq: JF694319 (actin) Lahr et al. 2011 Tr: SAMN02740475 (Keeling et al. 2014)
Squamamoeba Kudryavtsev and Pawlowski, 2013.						
Squamamoeba japonica	Kudryavtsev and Pawlowski 2013		CCAP 1593/1(T)	42.440562N, 133.145968E; soft bottom sediments of the Sea of Japan, Pacific Ocean; depth 2709 m		LM, EM, Seq: Kudryavtsev and Pawlowski 2013; JN638030-JN638032 (SSU rDNA), JN638033-JN638037 (COI) Tr: SAMN06642744; Kang et al. 2017

small number of taxa found only recently, may be due to the small size of these amoebae (generally below 10 µm) that makes them difficult to observe and isolate.

Evosea, Archamoebae, Mastigamoebida (Table 9).

***Mastigamoeba* Schulze, 1875.**

Evosea, Archamoebae, Pelobiontida (Table 10).

***Mastigella* Lemmermann, 1914.**

A few Archamoebae reported from marine environments have never been reinvestigated using molecular methods, and their identity in some cases remains ambiguous. This poor knowledge may be due to the fact that these clades comprise anaerobic amoeboflagellates, and marine anaerobic microbiota is poorly studied in general.

Discosea, Flabellinia, Thecamoebida (Table 11).

***Thecamoeba* Schaeffer, 1926.** This genus comprises freshwater, terrestrial and marine species, and its terrestrial diversity is best studied (Mesentsev and Smirnov, 2019, 2021; Mesentsev et al., 2020). However, five species were described from marine biotopes, with only morphological data available until now. We may expect the higher diversity in future if more microhabitats are surveyed.

Discosea, Flabellinia, Dermamoebida (Table 12).

***Mayorella* Schaeffer, 1926.** After a lot of taxonomic perturbations (Goodkov, 1988) this genus was finally separated from morphologically similar ones based on the cell coat structure, and transferred into Dermamoebida based on the molecular data. It is noteworthy that many of its marine species have never been reinvestigated since their initial descriptions that were published before the diversity within the genus *Mayorella* was realized. Therefore, their generic assignment should be treated with caution.

Discosea, Flabellinia, Dactylopodida (Table 13).

***Cunea* Kudryavtsev and Pawlowski, 2015.**

Three species of this genus were first described only recently, all from marine or continental brackish water biotopes (Kudryavtsev and Volkova, 2020). Interestingly, this is the only genus of Amoebozoa

Table 9. Evosea, Archamoeba, Mastigamoebida.

Species	Initial description	Redescriptions and earlier synonyms (if present)	Strains if available	Habitat	Salinity tolerance range	Data available
Mastigamoeba Schulze, 1875.						
<i>Mastigamoeba aspera</i>	Schulze 1875			Pond in botanical garden in Joanneum, Graz (Austria), freshwater (Schulze 1875) Ca. 44.02756N, 69.52809W, tidal pools, Day's Cove, Damariscotta River, Maine (US); salinity 29-30 ppt (Page 1970b) Ca. 58.58333N, 28.91667E, anaerobic bottom sediments of a freshwater forest lake near Lyady village, Pskov Region (Russia); ca. 60.55109N, 30.22313E, anaerobic bottom sediments of a freshwater forest lake near Sosnovo settlement, Leningrad Region (Russia) (Chistyakova et al. 2012)	If Page's (1970b) identification is correct, this is one of the few amoeba species that occur in sea- and freshwater biotopes simultaneously.	LM: Schulze 1875, Page 1970b LM, EM: Chistyakova et al. 2012
<i>Mastigamoeba psammobia</i>	Larsen and Patterson 1990			Ca. 19.28333S, 147.06666E, anaerobic mud in mangroves, Bowling Green Bay, Cape Fergusson (Australia), ca. 22.85346S, 43.21695W, anaerobic mud in mangroves, Ilha do Fundão, Rio de Janeiro (Brazil) (Larsen and Patterson 1990)		LM: Larsen and Patterson 1990
<i>Mastigamoeba simplex</i>	Calkins 1902	This name turns out to be a junior homonym of a freshwater species <i>Mastigamoeba simplex</i> Kent, 1880 later renamed <i>Mastigella simplex</i> Lemmermann, 1914. This is strange though, because Calkins cited Kent (1880) in his work.		Ca. 41.5252N, 70.67485W, decaying marine algae, Woods Hole, Massachusetts, US		LM: Calkins 1902

Table 10. Evosea, Archamoeba, Pelobiontida.

Species	Initial description	Redescription and earlier synonyms (if present)	Strains if available	Habitat	Salinity tolerance range	Data available
Mastigella Lemmermann, 1914.						
<i>Mastigella simplex</i>	Kent 1880	Lemmermann 1914; <i>Mastigamoeba simplex</i> (Kent 1880)		Pond water (Kent 1880) Ca. 19.28333S, 147.06666E, anaerobic mud in mangroves, Bowling Green Bay, (Australia) (Larsen and Patterson 1990)		LM: Kent 1880, Larsen and Patterson 1990

Table 11. Discosea, Flabellinia, Thecamoebida.

Species	Initial description	Redescription and earlier synonyms (if present)	Strains if available	Habitat	Salinity tolerance range	Data available
Thecamoeba Schaeffer, 1926.						
<i>Thecamoeba hilla</i>	Schaeffer 1926		CCAP 1583/1+	Irrigated marine cultures: Tortugas, Florida, US (Schaeffer 1926); 44.2098N, 69.05623W, seawater, rocky shore: Penobscot Bay, Camden, Maine (US) 30 ppt (Page 1971b)	3-30 ppt (growth and survival), Page 1971b, Schaeffer 1926	LM: Page 1971b, 1977, 1983a, Schaeffer 1926
<i>T. munda</i>	Schaeffer 1926			Marine, among blue-green algae: Key West Harbor, Florida, US; algal cultures in Tortugas Laboratory, Florida, US (Schaeffer 1926). 55.92054N, 12.52338E; upper layer of sediments (sand, anaerobic bacterial mats), Nivå Bay, The Sound, Denmark; 15 ppt (Smirnov 1999a,b)		LM: Schaeffer 1926 LM, EW: Smirnov 1999a,b
<i>T. orbis</i>	Schaeffer 1926		CCAP 1583/2+	Marine, floating sea-weeds, Tortugas, Florida, US (Schaeffer 1926). Edge of Damariscotta River at Damariscotta, Maine, US (Page 1971b)	3-30 ppt (survival), no recovery after 1.5 ppt (Schaeffer 1926) 3-30 ppt (growth), Page 1971b	LM: Schaeffer 1926, Page 1971b, 1977 LM, EM: Page 1983a, Page and Blakey 1979
<i>T. pulchra</i>	Biernacka 1963	Page 1977; Amoeba pulchra (Biernacka 1963)		Ca. 54.4051N, 18.83246E, Bay of Gdansk, Baltic Sea (Poland), salinity 6.5-7.5 ppt.		LM: Biernacka 1963
<i>T. rugosa</i>	Schaeffer 1926			Marine, among blue-green algae: Key West Harbor, Florida, US; seawater tank in Tortugas Laboratory, Florida, US	7.5-30 ppt (Schaeffer 1926)	LM: Schaeffer 1926

that currently comprises only sibling species with differences only in sequence data and ecological preferences.

Korotnevella Goodkov, 1988. Most of *Korotnevella* species are from freshwater, but known marine species suggest that their actual diversity may be higher.

Pseudoparamoeba Page, 1979. The known diversity of this genus is not broad at the moment; all species, except one are marine.

Vexillifera Schaeffer, 1926. The taxonomic diversity of this genus has been fully reviewed recently (Kudryavtsev et al., 2018); it is well represented in marine and freshwater biotopes, but many of the species were studied using light microscopy only. The phylogenetic relationships within the genus reconstructed using SSU rRNA gene suggest that there are two independent deeply-branching marine clades and one derived freshwater clade within this genus (Kudryavtsev et al., 2020).

Paramoeba Schaudinn, 1896, Neoparamoeba Page, 1987, and Janickina Chatton, 1953. These genera are exclusively marine. In the morphology-based classifications, Janickina was first separated from *Paramoeba* to accommodate species with PLO (“parasome”), but very different, limax-like locomotive forms. After data on cell coat ultrastructure became available, *Neoparamoeba* was established by Page (1987) to accommodate those species with PLO (“parasome”) that have no surface microscales. Page (1987) only listed *N. aestuarina* and *N. pemaquidensis* as species of *Neoparamoeba*. However, if the absence of surface microscales is the defining character of *Neoparamoeba* Page, 1987, then *P. perniciosus* Sprague et al., 1969 and *P. invadens* Jones, 1985 should also be included in this genus (discussed in Volkova et al., 2019). As this transfer was never done formally, we list these species under *Paramoeba*. As some of these species are parasites of fish and invertebrates that may be economically important, a considerable amount of molecular data on these amoebae has been generated recently. Phylogenetic analysis shows that the topology of this clade does not correspond to its morphological diversity. Therefore, the taxonomy of these genera requires emendation. In particular, the validity of *Neoparamoeba* Page, 1987 and *Janickina* Chatton, 1953 is debated recently. However, given the morphological and ecological heterogeneity of the clade comprising *Paramoeba*, *Neoparamoeba*, and *Janickina*, we provisionally retain all generic names to prevent loss of taxonomic diversity in the literature (Vokova et al., 2019; Volkova and Kudryavtsev, 2021).

Table 12. *Discosea*, *Flabellinia*, *Dermamoebida*.

Species	Initial description	Redescription and earlier synonyms (if present)	Strains if available	Habitat	Salinity tolerance range	Data available
<i>Mayorella</i> Schaeffer, 1926.						
<i>Mayorella conipes</i>	Schaeffer 1926			Seawater: Tortugas, Florida, Long Island Sound, Great South Bay, Long Island, New York, US (Schaeffer 1926)	9-35 ppt (survival)	LM: Schaeffer 1926
<i>M. corlissi</i>	Sawyer 1975a			Seawater: Chincoteague Bay near Greenbacksville, Virginia, Salt Pond, Woods Hole, Massachusetts, US (Bovee and Sawyer 1979)	No tolerance	LM: Sawyer 1975a, Bovee and Sawyer 1979
<i>M. crystallus</i>	Schaeffer 1926			Seawater tank, Tortugas Marine Laboratory, Florida (US)		LM: Schaeffer 1926
<i>M. dactylifera</i>	Goodkov and Buryakov 1988			Ca. 66.33518, 33.64777, artificial and natural submerged substrates around Cape Kartesh area, Kandalaksha Bay, the White Sea (Russia), 22-23 ppt		LM, EM: Goodkov and Buryakov 1988
<i>M. gemmifera</i>	Schaeffer 1926		CCAP 1547/8 1547/12	Seawater: Tortugas, Florida, Cold Spring Harbor, New York, US (Schaeffer 1926); ca. 52.94545N, 1.21765E, sandy beach at Sheringham, Norfolk, UK (CCAP 1547/8, https://www.ccap.ac.uk/catalogue/strain-1547-8 ; https://www.ccap.ac.uk/catalogue/strain-1547-12)		LM: Schaeffer 1926 LM, EM: Page 1983a, Dyková and Kostka 2013, Dyková et al. 2008c Seq: EU719190 (SSU rDNA) Dyková et al. 2008c
<i>M. kuwaitensis</i>	Page 1981b	Page 1983a; <i>Hollandella kuwaitensis</i> (Page 1981b)	CCAP 1547/9	Seawater tanks, Kuwait Institute for Scientific Research, Kuwait		LM, EM: Page 1981b, Page 1983a
<i>M. smalli</i>	Sawyer 1975a			Seawater: Chincoteague Bay near Greenbacksville, Virginia, US; 25.7-30.7 ppt		LM; Sawyer 1975a
<i>M. pussardi</i>	Hollande et al. 1981			Ca. 43.683N, 7.317E, Bay of Villefranche, Villefranche-sur-mer (France)		LM, EM: Hollande et al. 1981

Table 13. Discosea, Flabellinia, Dactylopodida.

Species	Initial description	Redescription and earlier synonyms (if present)	Strains if available	Habitat	Salinity tolerance range	Data available
Cunea Kudryavtsev and Pwłowski, 2015.						
<i>Cunea profunda</i>	Kudryavtsev and Pwłowski 2015		CCM 602/13/16(T)	3.9498333S, 28.087W, bottom sediments and overlying seawater, Brazilian abyssal plain (Western Atlantic ocean; depth 5169.3 m), 35 ppt	19-70 ppt, Kudryavtsev and Volkova 2020	LM, EM: Kudryavtsev, Pawłowski 2015. Seq: KP862834-KP862838 (SSU rRNA); KP862843-KP862846 (actin) KP862853-KP862855 (Cox1) Kudryavtsev and Pawłowski 2015.
<i>Cunea russae</i>	Kudryavtsev, Volkova 2020		CCM Am0458(T)	57.98318N, 31.33482E; bottom sediments of the brackish-water basin surrounding the Tsaritsinskiy Spring, town of Staraya Russa, Novgorod Region (Russia), 19ppt	2.5-50 ppt, Kudryavtsev and Volkova 2020	LM, EM: Kudryavtsev and Volkova 2020. Seq: MN317563-MN317566 (SSU rDNA), MN317568-MN317570 (actin), MN317567 (COI) Kudryavtsev, Volkova 2020.
<i>Cunea thuwala</i>	Kudryavtsev and Pwłowski 2015			22.31985N, 39.004684E; bottom sediments, Red Sea, Saudi Arabian coast, depth 58.7 m, salinity 40 ppt		LM, EM: Kudryavtsev, Pawłowski 2015. Seq: KP862839-KP862842 (SSU rDNA) KP862847-KP862851 (actin) KP862852 (Cox1) Kudryavtsev, Pawłowski 2015.
Korotnevelia Goodkov, 1988.						
<i>Korotnevelia nivo</i>	Smirnov 1996/97	This species may be an aparasomate Paramoeba (Volkova et al. 2019)		55.92054N, 12.52338E; upper layer of sediments (sand, anaerobic bacterial mats), Nivå Bay, The Sound (Denmark), 35 ppt		LM, EM: Smirnov 1996/97
<i>K. hemistylelepis</i>	O'Kelly et al. 2001		ATCC 50804(T)	37.73811N, 75.85958W; water samples at the mouth of the Pocomoke River, Chesapeake Bay, Maryland (USA)		LM, EM: O'Kelly et al. 2001 Seq: AY121850 (SSU rDNA) Peglar et al. 2003
<i>K. monocantholepis</i>	O'Kelly et al. 2001		ATCC 50819	Mesohaline marine aquarium maintained in the laboratory of Dr. Edward J. Noga at the Department of Veterinary Science, North Carolina State University, Raleigh, North Carolina (USA)		LM, EM: O'Kelly et al. 2001 Seq: AY121854 (SSU rDNA) Peglar et al. 2003
<i>K. mutabilis</i>	Udalov et. al 2020b		CCM Am0464(T)	55.92054N, 12.52338E; mesohaline marine sediment sample, Nivå Bay, The Sound (Denmark)	8-30 ppt (Volkova unpublished data)	LM, EM, Seq: MT193520 (COI): Udalov et. al 2020b
Pseudoparamoeba Page, 1979.						

Table 13. Continuation.

<i>Pseudoparamoeba pagei</i>	Sawyer 1975a	Page 1979b; <i>Vexillifera pagei</i> (Sawyer, 1975)	CCAP 1566/1, CCAP 1566/2+ (Page 1979b); ATCC 50883 (deposited as <i>Vexillifera armata</i> ; Peglar et al. 2003)	Seawater: Chincoteague Bay near Greenbacksville, Virginia, US; 25.7-30.2 ppt (Sawyer 1975a); CCAP 1566/2: ca. 44.2098N, 69.05623W; seawater, rocky shore: Penobscot Bay, Camden, Maine (US) 30 ppt CCAP 1566/1: ca. 50.2539N, 3.75267W; seawater, mud, Frogmore Creek, off the Kingsbridge estuary, Devon (UK) 50.21853N, 3.77491W; seawater, mud, Kingsbridge River estuary, Devon (UK) (Page 1979b) ATCC 50883: ca. 37.44458N, 75.84187W; salt marsh sediment at Red Bank LTER site, University of Virginia (US), Peglar et al. 2003	3-30 ppt (Sawyer 1975a)	LM: Sawyer 1975a LM, EM: Page 1979 Seq: AY183891 (SSU rDNA), Peglar et al., 2003; AY686576, AY277798 (SSU rDNA), Wong et al., 2004; MH349033-MH349037 (COI), CCAP 1566/1), MH349038-MH349044 (COI), CCAP 1566/2), Kudryavtsev et al. 2018	
<i>P. garorimi</i>	Udalov et al. 2020a		CCM Am0455(T)	36.92555N, 126.33916E, intertidal sandy surface sediments, Garorim Bay (South Korea), ca. 30 ppt		LM, EM, Seq: Udalov et al. 2020a; MK482386 (18S rDNA), MK482724 (COI)	
<i>Pseudoparamoeba</i> sp.	English et al. 2019		MX1 (not deposited)	Farmed Atlantic salmon, Tasmania (Australia)		LM, EM: English et al. 2019 Seq: MH535944 (COI), MH535967 (SSU rDNA) English et al. 2019.	
Vexillifera Schaeffer, 1926.							
<i>Vexillifera abyssalis</i>	Kudryavtsev et al. 2018		CCM A0006	Ca. 26.64S, 35.2395W, surface of a stone picked with Agassiz trawl, bottom of Brazilian abyssal plain, depth 4527 m, western Atlantic Ocean, ca. 35 ppt		LM, EM: Kudryavtsev et al. 2018 Seq: MH349019-MH349020 (SSU rDNA), MH349024-MH349027 (COI) Kudryavtsev et al. 2018	
<i>V. armata</i>	Page 1979a			Ca. 50.2539N, 3.75267W; seawater, mud, Frogmore Creek, off the Kingsbridge estuary, Devon (UK) (Page 1979a);		LM, EM: Page 1979a, 1983a	
<i>Vexillifera</i> cf. <i>armata</i>	Page 1979a		CCM Am 0466	42.69579N, 132.58841E; bottom sediment, Vostok Bay of the Sea of Japan, depth 70 m (Kudryavtsev et al. 2020)	15-50 ppt (growth), 10, 70-90 ppt (survival) (Kudryavtsev et al. 2020)	LM, EM: Kudryavtsev et al. 2020 Seq: MT228921, MT228922 (SSU rDNA), MT228923-MT228925 (COI), Kudryavtsev et al. 2020	
<i>V. aurea</i>	Schaeffer 1926			Seawater at Tortugas, Florida, and Cold Spring Harbor, Long Island (US)	18-35ppt (survival)	LM: Schaeffer 1926	
<i>V. browni</i>	Sawyer 1975a			Seawater: Chincoteague Bay near Greenbacksville, Virginia, US; 28.9-30.7 ppt	35 ppt, stenohaline species	LM: Sawyer 1975a	
<i>V. minutissima</i>	Bovee and Sawyer 1979		CCAP 1590/3, originally designated C64 (Page 1979a)	Isolated from shallow water (bays, estuaries) in Chincoteague Bay, Virginia; US eastern coast, Virginia to Massachusetts (Bovee and Sawyer 1979) Ca. 51.43645N, 3.1669W, mud, algal material, beach at Penarth, South Glamorgan (Page 1979a, 1983a)		LM: Bovee and Sawyer 1979, Page 1983a EM: Page 1979a, 1983a Seq: AY294149 (SSU rDNA), Fahmi et al., 2003; MH349031 (COI), Kudryavtsev et al. 2018	
<i>V. kereti</i>	Kudryavtsev et al. 2018		CCM A0007	66.291716N, 34.065166E, soft bottom sediments (upper reddish-brown mud layer), sublittoral area, outlet of Chupa Inlet, Kandalaksha Bay, White Sea (northwestern Russia); depth 106 m, salinity 29 ppt		LM, EM: Kudryavtsev et al. 2018; Seq: MH349021-MH349023 (SSU rDNA), MH349032 (COI), Kudryavtsev et al. 2018	

Table 13. Continuation.

V. ottoi	Sawyer 1975a			Seawater: Chincoteague Bay near Greenbacksville, Virginia, US; 25.7-32.6 ppt	30 ppt (growth and survival), stenohaline species	LM: Sawyer 1975a
V. tasmaniana	Dyková et al. 2011		CC RMT(T)	Ca. 41.40092S, 147.12314E, gills of the cultured Atlantic salmon Salmo salar, Launceston School of Aquaculture, University of Tasmania, Australia	27 ppt seawater, Dykova et al. 2011	LM, EM: Dyková et al. 2011, Dyková and Kostka 2013 Seq: HQ687483 (SSU rDNA) Dyková et al. 2011
V. teimathalassa	Bovee 1956b			Ca. 33.7969N, 118.40821W, water samples from mid-tide pools in volcanic rock at Flat Rock Point near Palos Verdes, California (US); ca. 29.10224N, 83.06204W, samples of seawater and sand from a tide-washed sandspit at Seahorse Key, Florida (US), Bovee 1956b Ca. 13.18413N, 59.67614W, seawater 4 km west of St. James, Barbados, depth ca. 1.5 m (Anderson 1994)	16-36 ppt (Anderson 1994)	LM: Bovee 1956b LM, EM: Anderson 1994
V. spinosa	Bovee 1985			Ca. 26.90764N, 82.08949W, brackish backwater of the Peace River at Punta Gorda, Florida (US)		LM: Bovee 1985
Vexillifera sp.	Pizzetti et al. 2016		K9 (not deposited)	Ca. 41.27008N, 13.0375E, surface seawater, Lago di Sabaudia, Tyrrhenian Sea coast, Latina (Italy), 33.7 ppt		LM, EM, Seq: LC049074 (SSU rDNA) Pizzetti et al. 2016
Vexillifera sp.	English et al. 2019		MX6 (not deposited)	Farmed Atlantic salmon, Tasmania (Australia)		LM, EM, Seq: MH535966 (SSU rDNA) MH535945 (COI) English et al. 2019
Paramoeba Schaudinn, 1896.						
Paramoeba eilhardi	Schaudinn 1896			Marine aquarium in Berlin, Germany (Schaudinn 1896) CCAP 1560/2: ca. 43.69604N, 7.30734E, algal material from The Bay of Villefranche (France) Grell 1961		LM: Cann and Page 1982, Grell 1961, Kudryavtsev et al. 2011a, Schaudinn 1896; EM: Cann and Page 1982, Grell and Benwitz 1966, Grell and Benwitz 1970, Kudryavtsev et al. 2011a Seq: AY686575 (SSU rDNA) Mullen et al. 2005; JN202438-JN202441 (SSU rDNA) Kudryavtsev et al. 2011a; MK168797-MK168799 (COI) Volkova et al. 2019; MH535952 (SSU rDNA) English et al. 2019
P. karteshi	Volkova et al. 2019		CCM Am0453(T)	66.3369944N, 33.6598806E, pieces of a sponge Halisarca dujardini, sublittoral of the Levaya Bay, Chupa Inlet, Kandalaksha Bay, White Sea (Russia), depth 5 m, salinity 24-27 ppt		LM, EM: Volkova et al. 2019 Seq: MK168787-MK168789 (SSU rDNA), MK168800-MK168802 (COI), Volkova et al. 2019.
P. aparasomata	Volkova et al. 2019		CCM Am0454(T)	66.321344N, 33.85184E Marine (24-27 ppt), sublittoral soft bottom sediments, island beach Chupa Inlet, Kandalaksha Bay, White Sea (Russia), depth 6 m, salinity 24-27 ppt		LM, EM: Volkova et al. 2019 Seq: MK168790-MK168793 (SSU rDNA), MK168803 (COI) Volkova et al. 2019 G: MK518072 (mitochondrial) Bondarenko et al. 2020
P. atlantica	Kudryavtsev et al. 2011		CCAP 1560/9(T)	29.604833N, 28.985333W, soft bottom sediments of the Great Meteor Seamount, Atlantic Ocean, depth 267.4 m, 35 ppt		LM, EM: Kudryavtsev et al. 2011 Seq: JN202436 (SSU rDNA) Kudryavtsev et al. 2011

Table 13. Continuation.

<i>P. invadens</i>	Jones 1985				Tissues of <i>Strongylocentrotus droebachiensis</i> from sublittoral zone, coast of Nova Scotia (Canada), 26 ppt, Jones 1985		LM; EM: Jones, 1985; Feehan et al., 2013, Seq: KC790384-KC790387 (SSU rDNA). Feehan et al., 2013; KY465820-KY465839 (SSU rDNA), Sibbald et al., 2017; KU609016 (uroporphyrinogen III synthase mRNA), Cenci et al., 2016;
<i>P. perniciosus</i>	Sprague et al. 1969				Chincoteague Bay, Maryland and Virginia, isolated form blood of crabs <i>Callinectes sapidus</i>	17-35ppt	LM; Sprague et al. 1969 EM: Perkins and Castagna 1971
<i>P. schaudinni</i>	Da Faria and Pinto 1922				Isolated form marine aquarium		LM: da Faria and Pinto 1922
Neoparamoeba Page, 1987.							
<i>Neoparamoeba aestuarina</i>	Page 1970a	Page 1987, Paramoeba aestuarina (Page 1970a)	CCAP 1560/7+, ATCC 50744, ATCC 50805(+), ATCC 50806(+), CCM A0005, CC SU03		Ca. 44.02756N, 69.52809W, sand, water and algal washes from tidal marsh in Days Cove, Damariscotta River, Maine (US), Page 1970a; CCAP 1560/7: east of Atlantic Ocean (Portugal) https://www.ccap.ac.uk/catalogue/strain-1560-7 ATCC 50744: ca. 37.96876N, 76.31482W, Potomac River estuary, Virginia (US); ATCC 50805: ca. 37.44896N, 75.67268W, Hog Island, Virginia (US); ATCC 50806: 38.30871N, 76.40357W, Patuxent River estuary, Maryland (US), Peglar et al. 2003 CCM A0005: 42.271593N, 136.73835E, soft sediment samples, Sea of Japan, depth 3665 m (Volkova and Kudryavtsev 2017) CC SU03: ca. 43.28517N, 16.87264E, radial water vessels of a purple sea urchin, <i>Sphaerechinus granularis</i> off the Brač Island, Adriatic Sea (Croatia) Dyková et al. 2008b	estuarine cultivated at 30 ppt sea-water (Page, 1970a)	LM; Page, 1970a; Page 1983a EM: Page 1983a Seq: EU331035 (SSU rDNA), Dyková et al. 2008b; AY121848, AY121851, AY121852 (SSU rDNA) Peglar et al. 2003; AF371973 (SSU rDNA) Wong et al. 2004; AY686574 (SSU rDNA) Mullen et al. 2005; MF197372-MF197374 (SSU rDNA) Volkova and Kudryavtsev 2017; AY743963-AY743964 (cyfB) Lin and Zhang 2005; DQ167554 (ITS1-5.8S-ITS2, partial LSU rDNA) Caraque et al. 2007; EU884481-EU884483, (ITS1-5.8S-ITS2) Young et al. 2014
<i>N. aestuarina antarctica</i>	Moran et al. 2007		Not deposited: S-131-2 SL-200 W4-3		S-131-2: 76.59933S, 165.002667W, sediment, Ross Sea, Antarctica, depth 500 m; SL-200: 71.005333S, 135.063833W, slush in the pack ice, Ross Sea, Antarctica; W4-3: 65.241667S, 165.2255W, water sample from combined depths, far north edge of the Ross Sea pack ice, Antarctica.		Seq: DQ229957-DQ229959 (SSU rDNA), Moran et al., 2007

Table 13. Continuation.

<p>N. permaquidensis</p>	<p>Page, 1970</p>	<p>CCAP 1560/4 1560/5+ ATCC 50172 CC AF5M11 FRS GILLNOR1 GILLNOR2 LITHON NET12AFL NETH2T3 NP251002 PA027 SEDC SEDST1 ST8V TUN1 WTZ708 WTUTS Not deposited: ASL1 FHL GILLRICH3 NETC1 NETC2 PAL2 SEDCB1 SEDSA TGI1267 UA1 UA6</p>	<p>Ca. 43.87116N, 69.52037W, sand, water, and algal washings, lower intertidal zone, Pemaquid beach, Maine (US) Page 1970; CCAP 1560/4, 1560/5: ca. 52.91695N, 4.2107W, Criccieth, Gwynedd, Wales, UK (https://www.ccap.ac.uk/catalogue/strain-1560-4; https://www.ccap.ac.uk/catalogue/strain-1560-5); ATCC 50172: ca. 47.72365N, 122.47133W, Puget Sound, Washington (US) Peglar 2003 (no records on this strain are available in ATCC web page); AF5M11: gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain (Dyková et al. 2005b) AVG 8194: gills of AGD-affected cultivated Atlantic salmon (<i>Salmo salar</i>) in Ireland (Wong et al. 2004) FHL: ca. 48.49406N, 123.00152W, tidal mud flat at San Juan Island, Washington (US) Sibbald et al. 2017 ASL1, FRS, NP251002, WTUTS: ca. 41.40092S, 147.12314E, gills of the cultivated Atlantic salmon (<i>Salmo salar</i>), Launceston School of Aquaculture, University of Tasmania (Australia) Dyková et al. 2005b, Young et al. 2014 GILLNOR1, GILLNOR2: ca. 43.21581S, 147.30048E, gills of Atlantic salmon <i>Salmo salar</i>, D'Entrecasteaux Channel, Bruny Island, Tasmania, Australia LITHON: ca. 63.00002N, 7.29224E, red alga <i>Lithophyllum racemosum</i> surface off Vevang, Trondheim (Norway) Dyková et al. 2008b NET12AFL, NETC1, NETC2, NETH2T3: ca. 43.31248S, 147.08289E, cage net, fish farm, Huon estuary, Dover, southeast Tasmania (Australia) Dyková et al. 2005b, Dyková et al. 2008b PA027, ST4N, ST8V, WTZ708: ca. 43.31248S, 147.08289E, Dover, southeast Tasmania (Australia) Dyková et al. 2008b Huon estuary, Dover, southeast Tasmania (Australia) Dyková et al. 2008b, Wong et al. 2004 SEDC: ca. 41.88133S, 148.3157E, sediment under the <i>Salmo salar</i> sea cage, Bicheno, Tasmania (Australia) Dyková et al. 2005b SEDCB1: ca. 43.33871S, 147.02928E, sediment under the <i>Salmo salar</i> sea cage, Stringers Cove, Tasmania (Australia) Dyková et al., 2005b SEDS5A: ca. 43.09843S, 147.72325E, sediment under the <i>Salmo salar</i> sea cage, Wedge Bay, Tasmania (Australia) Dyková et al. 2005b SEDC1T1: ca. 41.06686S, 146.78644E, sediment under the <i>Salmo salar</i> sea cage, River Tamar estuary, Tasmania (Australia) Dyková et al. 2005b TUN1, TGI162, TGI267: ca. 34.71106S, 135.86313E, gills of a dead Southern Bluefin tuna (<i>Thunnus maccoyii</i>), Port Lincoln, (Australia) Dyková et al. 2007b GILLRICH3: gills of Atlantic salmon (<i>Salmo salar</i>), Tasmania (Australia) Dyková et al. 2007b PAL2: ca. 63.00002N, 7.29224E, surface of algae, <i>Palmaria palmata</i>, Vevang, Trondheim (Norway) Young et al. 2014 UA1, UA6: sea urchin <i>Strongylocentrotus droebachiensis</i>, Gulf of Maine (US) Caraguel et al. 2007</p>	<p>LM: Page 1970, 1973, Young et al. 2014 LM, EM: Cann and Page 1982, Dyková and Kostka 2013, Dyková et al. 2000, 2003, 2005b, 2007b, 2008b, Page 1983a, Sibbald et al. 2017, Tanifuji et al. 2011 Seq: JF706697 (rpbl), JF706698, JF262548 (tuba), JF262553 (tubb), JF441171 (trans-spliced leader SL gene) Tanifuji et al. 2011; DQ660492, DQ167506-DQ167553 (SSU rDNA, ITS1, 5.8S, ITS2, LSU rDNA), Caraguel et al. 2007; AF371967-AF371972 (SSU rDNA), Wong et al. 2004; EU884493-EU884494 (SSU rDNA), Young et al. 2014; EU331036, EU331021 (SSU rDNA) Dyková et al., 2008b; EF675601, EF675602, EF675604-EF675607 (SSU rDNA), Dyková et al. 2007b; AY714350-AY714364 (SSU rDNA) Dyková et al. 2005b; AY183887, AY183889, AY183894 (SSU rDNA) Peglar et al. 2003; AY743964 (cob), Lin and Zhang 2005; EU884447; EU884450-EU884461, EU884465-EU884466, EU884473-EU884477, EU884479, EU884486-EU884490, EU884492 (ITS1-5.8S-ITS2) Young et al. 2014; EF216898, EF216912, EF216913, EF216915 (LSU rDNA) Young et al. 2007 KY465848-KY465852 (SSU rDNA) Sibbald et al., 2017; KU609011-KU609043 (various markers), Cenci et al. 2016; KF772980 (EF1a), KF772979 (beta actin), Lima et al. 2014; MN025475, MK990593 (COI) Hansen et al. 2019 G: MUHK01000000 (nuclear genome), NC_031417, KX611830 (mitochondrial complete genome) Tr: GEWA01000000; Tanifuji et al. 2017</p>
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Table 13. Continuation.

N. branchiphila	Dyková et al., 2005b	CC AF5M3 AMOPI NRSS RP SEDMH1 SM68+ ST4N S04 Not deposited: SM53 SM57	AF5M3, SM53, SM57, SM68: gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain (Dyková et al. 2005b) AMOPI: ca. 35.52159N, 27.2065E, sea urchin <i>Paracentrotus lividus</i> collected in Cretan Sea, Karpathos Island (Greece) Dyková et al. 2007b NRSS: ca. 41.40092S, 147.12314E, gills of the cultivated Atlantic salmon (<i>Salmo salar</i>), Launceston School of Aquaculture, University of Tasmania (Australia) Dyková et al. 2005b RP: ca. 30.37854N, 88.81847W, blue crab, <i>Callinectes sapidus</i> , Gulf of Mexico coast, Biloxi, Mississippi (US) Dyková et al. 2007b SEDMH1: ca. 42.17405S, 145.31038E, sediment under cages with cultured <i>Salmo salar</i> , Maquarie Harbour, Tasmania (Australia) Dyková et al. 2005b ST4N: ca. 43.31248S, 147.08289E, gills of cultured <i>Salmo salar</i> , fish farm, Huon estuary, Dover, southeast Tasmania (Australia) Dyková et al. 2005b SU4: ca. 41.06686S, 146.78644E, sea urchin <i>Heliocidaris erythrogramma</i> , River Tamar estuary, Tasmania (Australia) Dyková et al. 2007b OS, 5G5, KPF3: ca. 19.72676N, 156.06186W, seawater, sediment, and seaweeds, Keahole Point, the Big Island, Hawai'i (US) Sibbald et al. 2017	LM, EM: Dyková and Kostka 2013, Dyková et al. 2000, 2005b, 2007b, Fiola and Dyková 2003 Seq: AY193725 (SSU rDNA) Fiola and Dyková 2003; HQ132923-HQ132930, AY714365-AY714367 (SSU rDNA) Dyková et al. 2005b; EF216914-EF216918 (SSU rDNA) Young et al. 2007; EF675599 – EF675603 (SSU rDNA) Dyková et al. 2007b; KY465831-KY465847 (SSU rDNA) Sibbald et al. 2017; EU884448, EU884449, EU884462-EU884464, EU884478, EU884480, EU884484, EU884485, EU884491 (ITS1, 5.8S, ITS2) Young et al. 2014; FJ807261 (EF1A) Gile et al. 2009; MK990594 (COI) Hansen et al. 2019.
N. perurans	Young et al., 2007	SAUT GD-D1/2, GD-D1/1/1, GD-D1/3, GD-D1/4, GD-D1/1/2, GD-HAC/2/1, GD-HAC/2/2. Not deposited: 41XB 265VA 2795VA 82HRT MP1 MP2 IRE_2017_01 IRE_2017_02 IRE_1997_17_01A IRE_1997_17_01B NO_2006_09_01A NO_2006_09_01B NO_2013_17_01 NO_2013_17_06 NO_2014_17_01 NO_2014_17_02 SCO_2014_01 SCO_2016_01 SCO_2012_01A SCO_2012_02 SCO_2012_02 SCO_2012_01B SCO_2014_02A SCO_2014_02B TAS_2013 TAS_2015_41XB TAS_2015_265VA TAS_2015_82HRT TAS_2015_MP1 TAS_2015_MP2	All GD- strains: ca. 43.21581S, 147.30048E, gills of AGD-affected <i>Salmo salar</i> , D'Entrecasteaux Channel, Tasmania (Australia) Young et al. 2007 265VA, 2795VA, 41XB, 82HRT MP1, MP2: gills of AGD-infected <i>Salmo salar</i> farmed in Tasmania (Australia) English et al. 2019 Rest of the listed strains: samples of AGD recorded in Ireland (IRE), Norway (NO), Scotland (SCO), and Tasmania (TAS) Hansen et al. 2019	LM, EM: English et al. 2019, Young et al. 2007 Seq: EF216899-EF216905 (SSU rDNA) Young et al., 2007; EU326494 (SSU rDNA) Nylund et al., 2008; EU424141 (SSU rDNA) Martínez A. 2008, unpublished data; KT989880, KT989881 (SSU rDNA), Stagg et al. 2015; KF146711-KF146713 (SSU rDNA) Karlsbakk et al., 2013; KF179520 (SSU rDNA) Nylund et al. 2013; unpublished data; GU574794 (SSU rDNA) Nowak et al. 2010; EF216899-EF216905 (SSU rDNA) Young et al. 2007; KU985055-KU985058, (SSU rDNA) Kirm et al. 2016; EF216906-EF216918 (LSU rDNA) Young et al. 2007; GQ407108 (SSU rDNA) Bustos et al. 2011; GU574794 (LSU) Young et al. 2007; EU089662 (mRNA, actin), Morrison et al. 2007, unpublished data; EU884467-EU884472 (ITS1, 5.8S, ITS2) Young et al. 2008; MH535959, MH535962, MH535963 (SSU rDNA), MH535932, MH535934, MH535940, MH535946, MH535948 (COI) English et al. 2019; MN025476-MN025479 (COI) Hansen et al. 2019; MN010335-MN010353, MN010362-MN010376; MN010377-MN010379, MN010354-MN010361 (ITS) Hansen et al. 2019; MN025480-MN025488, MK990580 MK990577-MK990579; MN025489- MN025492, MK990581-MK990592; MH535932, MH535934, MH535940, MH535948, MH535946 (COI) Hansen et al. 2019
Neoparamoeba longipodia	Volkova and Kudryavtsev 2017	14.9785S, 29.95833W, bottom sediments, Brazilian abyssal plain, Western Atlantic Ocean, depth 5125.5 m, 35 ppt	LM, EM: Volkova and Kudryavtsev 2017. Seq: MF197368-MF197371 (SSU rDNA), MF140256 (COI) Volkova and Kudryavtsev 2017.	

Table 13. Continuation.

Neoparamoeba sp.		66KRT, 73BVA English et al. 2019		Seq: MH535953 (SSU rDNA), MH535938, MH535938 (COI) English et al 2019
Janickina Chatton, 1953.				
J. chetognathi	Grassi 1881	Chatton 1953; Amoeba chetognathi (Grassi 1881), Paramoeba chetognathi (Janicki 1912)	Caudal cavity of chaetognaths, Strait of Messina (Grassi 1881), Gulf of Naples (Janicki 1912); Mediterranean Sea	LM: Grassi 1881, Janicki 1912
J. pigmentifera	Grassi 1881	Chatton 1953; Amoeba pigmentifera (Grassi 1881), Paramoeba pigmentifera (Janicki 1912)	Caudal cavity of chaetognaths, Strait of Messina (Grassi 1881), Gulf of Naples (Janicki 1912), Bay of Villefranche (Hollande 1980, Volkova and Kudryavtsev 2021); Mediterranean Sea	LM: Grassi 1881, Janicki 1912, Volkova and Kudryavtsev 2021 EM: Hollande 1980 Seq: MZ021301- MZ021302 (SSU rDNA) Volkova and Kudryavtsev 2021

Discosea, Flabellinia, Vannellida (Table 14).

Clydonella Sawyer, 1975, *Lingulamoeba* Sawyer, 1975, and *Vannella* Bovee, 1965. The first two genera comprise exclusively marine species, while the third one, species from all habitats. Although validity of some of these genera was debated (Page, 1983a), they all were shown to be valid with combination of morphological and molecular data (Peglar et al., 2003; Dyková et al., 2005a). Instead, the genus *Platyamoeba* Page, 1969 was abandoned as a junior synonym of *Vannella* (Smirnov et al., 2007). As *Vannella* is probably one of the most frequently isolated genera of marine amoebae, the number of its unnamed marine strains is about twice as large as the number of its named marine species. Generic assignment of some species of *Clydonella* described earlier requires validation.

Discosea, Stygamoebida (Table 15).

Stygamoeba Sawyer, 1975, *Vermistella* Moran et al. 2007. The genera *Stygamoeba* and *Vermistella* comprising only marine species are classified together (Smirnov et al., 2011; Adl et al., 2019) in spite of the fact that they branch separately in most phylogenetic and phylogenomic trees (e.g. Lahr et al., 2011; Tymel et al., 2016; Kang et al. 2017). Before the sequence data for *S. regulata* were obtained, *Vermistella* was even considered a junior synonym of *Stygamoeba* (Smirnov, 2009) due to a striking morphological similarity of the two genera. In the tree by Lotonin and Smirnov (2020) both genera branch together, but the taxon sampling of that tree is very limited. Clearly, a more extensive study involving more species of amoebae belonging to this morphological group is needed to determine their phylogenetic affinities and a proper place in the classification system.

Discosea, Centramoebia, Acanthopodida (Table 16).

Acanthamoeba Volkonsky, 1930, *Protacanthamoeba* Page, 1981. The problem of the geographic distribution of *Acanthamoeba* in various environments is one of the most complicated. This genus is considered to be ubiquitous due to an ability to form robust cysts that can survive harsh environmental conditions, including salinity alterations (Page, 1983a). Therefore, many cases of isolation of fresh-water and soil species of *Acanthamoeba* from brackish and marine environments were reported.

Table 14. *Discosea*, *Flabellinia*, *Vannellida*.

Species	Initial description	Redescription and earlier synonyms (if present)	Strain if available	Habitat	Salinity tolerance range	Data available
<i>Clydonella Sawyer, 1975.</i>						
<i>Clydonella vivax</i>	Schaeffer 1926	Sawyer 1975c; <i>Rugipes vivax</i> (Schaeffer 1926)		Seawater: Tortugas, Florida, US; tidal pool: Cold Spring Harbor, Long Island, US (Schaeffer 1926) Seawater: Chincoteague Bay near Greenbacksville, Virginia, US; 26-30 ppt (Sawyer 1975a)	15-30 ppt (Sawyer 1975c)	LM; Schaeffer 1926, Sawyer 1975c
<i>C. rosenfieldi</i>	Sawyer 1975b			Seawater: Chincoteague Bay near Greenbacksville, Virginia, US; 29-30.2 ppt (Sawyer 1975a)	7.5-30 ppt	LM; Sawyer 1975b
<i>C. sawyeri</i>	Kudryavtsev and Volkova 2018		CCIM A0009(T)	66.3384387N, 33.618127E; upper layer of littoral mud and sand with bacterial mats: Chupa Inlet, Kandalaksha Bay, The White Sea, Russia; 22 ppt	5-50 ppt	LM, EM, Seq: Kudryavtsev and Volkova 2018 (SSU rDNA: MG559729-MG559731; COI: MG559732)
<i>C. sindermanni</i>	Sawyer 1975b			Seawater: Chincoteague Bay near Greenbacksville, Virginia, US; 30.7 ppt (Sawyer 1975a)	7.5-30 ppt	LM; Sawyer 1975b
<i>C. wardi</i>	Sawyer 1975b			Seawater: Chincoteague Bay near Greenbacksville, Virginia, US; 25.7-29 ppt (Sawyer 1975a)	22.5-30 ppt	LM; Sawyer 1975b
<i>Clydonella</i> sp. ATCC 50884	Peglar et al. 2003		ATCC 50884	Ca. 37.46597N, 75.70298W, salt marsh sediment, Chimney Pole, Virginia (US)		Seq: AY183892 (SSU rDNA) Peglar et al. 2003 Tr: SAMN04573363 (Tekle et al. 2016)
<i>Clydonella</i> sp. ATCC 50816	Peglar et al. 2003	Although this strain belongs to <i>Clydonella</i> according to molecular analysis by Peglar et al. (2003), ATCC lists it as <i>Vannella langae</i> (https://www.atcc.org/products/50816)	ATCC 50816	Ca. 37.44896N, 75.67268W, Hog Island, Virginia (US)		EM; Peglar et al. 2003 Seq: AY183890 (SSU rDNA) Peglar et al. 2003
<i>Lingulamoeba Sawyer, 1975.</i>						
<i>Lingulamoeba leei</i>	Sawyer 1975b		ATCC 30734	Seawater: Chincoteague Bay near Greenbacksville, Virginia, US; 32.6 ppt (Sawyer 1975b)	20-32.6 ppt (Sawyer 1975b)	LM; Sawyer 1975b EM, Seq: Peglar et al. 2003 (SSU rDNA: AY183886)
<i>Lingulamoeba</i> sp. RSH1	Dyková and Kostka 2013		CC RSH1	Ca. 41.40092S, 147.12314E, gills of the cultivated Atlantic salmon (<i>Salmo salar</i>), Launceston School of Aquaculture, University of Tasmania (Australia)		LM, EM, Seq: JQ271690 (SSU rDNA) Dyková and Kostka 2013
<i>Lingulamoeba</i> sp. RSL	Dyková et al. 2005a	Smimov et al. 2007 (originally <i>Vannella</i> sp.)	CC RSL	Ca. 41.40092S, 147.12314E, gills of the cultivated Atlantic salmon (<i>Salmo salar</i>), Launceston School of Aquaculture, University of Tasmania (Australia)		LM, EM; Dyková and Kostka 2013, Dyková et al. 2005a Seq: AY929908 (SSU rDNA) Dyková et al. 2005a

Table 14. Continuation.

Vannella Bovee, 1965.										
<i>Vannella aberdonica</i>	Page 1980a		ATCC 50815 (Peglar et al. 2003)	Ca. 57.15384N, 2.07809W; beach at Aberdeen, UK (Page 1980a). Ca. 38.63456N, 76.32661W; Choptank River, Maryland, US (Peglar et al. 2003)			LM, EM: Page 1980a Seq: AY121853 (SSU rDNA), Peglar et al. 2003			
<i>V. anglica</i>	Page 1980a		CCAP 1589/8, 1589/11(T)	52.313116N, 1.676647E; Brackish channel, Walberswick (UK); River Don estuary, Aberdeen (UK)			LM, EM: Page 1980a Seq: AF099101 (SSU rDNA), Sims et al. 1999; AF464913 (SSU rDNA), Sims et al. 2002			
<i>V. arabica</i>	Page 1980a		CCAP 1589/7	Kuwait Institute for Scientific Research seawater tank, presumably Gulf of Persia (Kuwait)			LM: Page 1980a, Smirnov et al. 2007 EM: Page 1980a Seq: AF464915 (SSU rDNA), Sims et al. 2002; EF051194 (SSU rDNA), Smirnov et al. 2007; GQ265392- GQ265397 (SSU rDNA), GQ265447- GQ265459 (ITS-5.8S), GQ354165- GQ354170 (COI), Nassonova et al. 2010			
<i>V. australis</i>	Page 1983a	Smirnov et al. 2007; <i>Platyamoeba australis</i> (Page, 1983a)	CCAP 1565/9 (T)+	Strain 236: Maroochydore, north of Brisbane, Pacific coast of Australia (Page 1980b)			LM: Page 1983a, Smirnov et al. 2007 EM: Page 1980b ("Strain 236") Seq: EF051199 (SSU rDNA), Smirnov et al. 2007			
<i>V. bursella</i>	Page 1974a	<i>Platyamoeba bursella</i> (Page 1974); Smirnov et al. 2007	CCAP 1565/5 (T)+, from strain 106; 1565/10, from strain 164	Strain 106: ca. 52.97572N, 0.63597E; seawater, sand, occasional macroalgae: sandy shore near Brankaster, Norfolk, UK. Strain 164: ca. 51.98332N, 1.39328E; seawater, mud, occasional macroalgae: low intertidal zone, River Deben estuary, UK; 29.5 ppt		3.5-35 ppt (strain 106) 9-35 ppt (strain 164) (Page 1974a)	LM: Page 1974a, Smirnov et al. 2007 EM: Page 1980b (strain 106) Seq: EF051195 (SSU rDNA), Smirnov et al. 2007; GQ265375- GQ265379 (SSU rDNA), GQ265441- GQ265446 (ITS-5.8S), GQ354148- GQ354153 (COI), Nassonova et al. 2010			
<i>V. caledonica</i>	Page 1979b			Strains 212, 213: River Morar estuary, UK			LM, EM: Page 1979b			
<i>V. calycinucleolus</i>	Page 1974a	<i>Platyamoeba calycinucleolus</i> (Page, 1974); Smirnov et al. 2007	CCAP 1565/6+, from strain 140	Strain 140: ca. 51.7733N, 0.9182E; seawater, sand, occasional macroalgae from 3 separate tidal pools, West Mersea, UK		9-35 ppt (strain 140)	LM: Page 1974a, Smirnov et al. 2007 EM: Page 1980b Seq: EF051193 (SSU rDNA), Smirnov et al. 2007; GQ265363- GQ265368 (SSU rDNA), GQ265435- GQ265440 (ITS-5.8S), GQ354136- GQ354141 (COI), Nassonova et al. 2010			
<i>V. contorta</i>	Moran et al. 2007	<i>Platyamoeba contorta</i> (Moran et al. 2007), Smirnov et al. 2007	W51C#4; ATCC PRA-217(T); W51C#5; ATCC PRA-218(T)	Strains W51C#4, W51C#5: 65.24166S, 165.225W, seawater, far north edge of the Ross Sea pack ice, Antarctic; depth 10 m (Moran et al. 2007)			LM, EM: Moran et al. 2007 Seq: DQ229953- DQ229954 (SSU rDNA), Moran et al. 2007			
<i>V. crassa</i>	Schaeffer 1926	Smirnov et al. 2007; <i>Flabellula crassa</i> (Schaeffer, 1926)		Irrigated cultures: Tortugas, Florida, US (Schaeffer 1926)		3.5-35 ppt (Schaeffer 1926)	LM: Schaeffer 1926			
<i>V. danica</i>	Smirnov et al. 2007		CCAP 1589/17(T)	Artificial laboratory cyanobacterial mat inoculated with material from: 55.92054N, 12.52338E; Nivå Bay, The Sound, Denmark (Smirnov et al. 2002)		0-50 ppt (Smirnov et al. 2002)	LM: Smirnov et al. 2002 (as <i>Vannella simplex</i> Nivå isolate), Smirnov et al. 2007 EM: Smirnov et al. 2002 (as <i>Vannella simplex</i> Nivå isolate) Seq: EF051203- EF051206 (SSU rDNA), Smirnov et al. 2007; GQ265386- GQ265391 (SSU rDNA), GQ265521- GQ265527 (ITS-5.8S), GQ354159- GQ354164 (COI), Nassonova et al. 2010			
<i>V. devonica</i>	Page 1979b		CCAP 1589/5(T)+	Ca. 50.2185N, 3.7749W, seawater, mud: Kingsbridge River estuary, Devon, UK (Page 1979b)			LM: Page 1979b, 1983a; Smirnov et al. 2007 EM: Page 1979b, 1983a Seq: EF051196 (SSU rDNA), Smirnov et al. 2007			

Table 14. Continuation.

V. douvresi	Sawyer 1975b	Smirnov et al. 2007;		Seawater: Chincoteague Bay near Greenbacksville, Virginia, US; 30.2 ppt (Sawyer 1975a)	7.5-30 ppt (Sawyer 1975b)	LM: Sawyer 1975b
V. ebro	Smirnov 2001			Stratified cyanobacterial mats in the system of natural channels: ca. 40.70003N, 0.84762E, Ebro River delta, Spain; salinity 70-80 ppt; depth 0.2-0.3 m	Reproduction: 6-90 ppt Survival: up to 135 ppt (Smirnov 2001)	LM, EM: Smirnov 2001 Seq: AF486084 (SSU rDNA), Smirnov et al. 2002; EF051198 (SSU rDNA), Smirnov et al. 2007; AY294151 (actin), Fahrni et al. 2003; MN095727 (COI), Kudryavtsev et al. 2019
V. langae	Sawyer 1975b	Smirnov et al. 2007; Platyamoeba langae (Sawyer 1975b)	ATCC 50816 (designated Cydonella sp. in Peglar et al. 2003)	Seawater: Chincoteague Bay near Greenbacksville, Virginia, US; 29.5-30.2 ppt (Sawyer 1975a)	7.5-30 ppt (Sawyer 1975b)	LM: Sawyer 1975b
V. mainensis	Page 1971b	Smirnov et al. 2007; Platyamoeba mainensis	CCAP 1565/1(T)+	Edge of Damariscotta river, Damariscotta, Maine, US; 30 ppt	Freshwater – 30 ppt (Page 1971b)	LM: Page 1971b, 1983a EM: Page 1980b
V. mira	Schaeffer 1926	Bovee 1965; Fiabelulia mira	CCAP 1589/15(T)+	Seawater, with cyanobacteria and decomposing material: Tortugas Marine Laboratory, Key West Harbor, US (Schaeffer 1926). Cyanobacterial mats with underlying sediment: Camargue Natural Reserve, France; 50 ppt (Smirnov 2002)	1.7-350 ppt (Hopkins 1938)	LM: Schaeffer 1926, Smirnov 2002 EM: Smirnov 2002
V. murchelanoi	Sawyer 1975b	Smirnov et al. 2007; Platyamoeba murchelanoi		Seawater: Chincoteague Bay near Greenbacksville, Virginia, US; 29.5-32.6 ppt (Sawyer 1975a)	7.5-30 ppt (Sawyer 1975b)	LM: Sawyer 1975b
V. nucleolliateralis	Anderson et al. 2003	Smirnov et al. 2007; Platyamoeba nucleolliateralis	ATCC 50987	Moist salt marsh sediment ca. 200 m away from the ocean, wildlife refuge on Assateague Island, Virginia, US	2.5-25 ppt (Anderson et al. 2003)	LM, EM: Anderson et al. 2003
V. oblongata	Moran et al. 2007	Smirnov et al. 2007; Platyamoeba oblongata	ATCC PRA-315(T)	71.99233S, 134.97399W, bottom sediment, Ross Sea, Antarctica; depth 3800 m		LM, EM: Moran et al. 2007 Seq: DQ229955 (SSU rDNA), Moran et al. 2007
V. peregrina	Smirnov and Fenchel 1996			55.92054N, 12.52338E; upper layer of sediments (sand, anaerobic bacterial mats), Nivå Bay, The Sound, Denmark (Smirnov and Fenchel 1996)		LM, EM: Smirnov and Fenchel 1996
V. plurinucleolus	Page 1974a	Smirnov et al. 2007; Platyamoeba plurinucleolus	117, 150, 151, 158; 139 (CCAP 1565/11)(T)	Sand, mud and algae from sandy beaches: CCAP 1565/11 (139): West Mersea, Essex, UK; 117: edge of water at high tide, Hunstanton, Norfolk, UK; 150, 151: pool next to grovne on beach, Holland-on-Sea, Essex, UK; 158: water's edge on beach with tide coming in, Harwich, Essex, UK (Page 1974a)	CCAP 1565/11, 150, 151, 158: 3.5-35 ppt (Page 1974)	LM: Page 1974a, Page 1983a, Smirnov et al. 2007 EM: Page 1980b Seq: EF051189 (SSU rDNA), Smirnov et al. 2007
V. pseudovannellida	Hauer et al. 2001	Smirnov et al. 2007; Platyamoeba pseudovannellida (Hauer et al. 2001)		Seawater with suspended particles near shore, Salton Sea, California, US; 44 ppt	0-138 ppt	LM, EM: Hauer et al. 2001

Table 14. Continuation.

<i>V. salina</i>	Ruinen and Baas Becking 1938	Kudryavtsev et al. 2019; <i>Fiabellula salina</i> (Ruinen and Baas Becking 1938)		Ca. 19.01671N, 72.87897E, salt works at Dadar near Bombay, India, 30-100 ppt.				LM; Ruinen and Baas Becking 1938
<i>V. samoroda</i>	Kudryavtsev et al. 2019		RC CCMAm 0457(T)	49.09618N, 46.73131E, hypersaline water and upper level of bottom sediment, mouth of the Malaya Samoroda River, Lake Elton, Volgograd Region (Russia); salinity ca. 110 ppt	Survival: 0-160 ppt Reproduction: 18-160 ppt		LM, EM: Kudryavtsev et al. 2019 Seq: MK992740-MK992743 (SSU rDNA), MK992744-MK992746 (actin), MN095725-MN095726 (COI), Kudryavtsev et al. 2019	
<i>V. sensilis</i>	Bovee 1950	Sawyer 1975; <i>Fiabellula sensilis</i> (Bovee 1950)		Atlantic and Pacific coasts of North America (Bovee and Sawyer 1979)			LM; Bovee 1953; Bovee and Sawyer 1979; Sawyer 1975c	
<i>V. septentrionalis</i>	Page 1980a		CCAP 1589/10(T+)	Ca. 57.15384N, 2.07809W; littoral sand and organic material, Don River estuary, Aberdeen, UK (Page 1980a).			LM, EM: Page 1980a, 1983; Smirnov et al. 2007 Seq: EF051197 (SSU rDNA), Smirnov et al. 2007	
<i>V. weinsteini</i>	Sawyer 1975b	Smirnov et al. 2007; <i>Platyamoeba weinsteini</i> (Sawyer, 1975)		Seawater, Chincoteague Bay near Greenbackville, Virginia, US; 30.7 ppt (Sawyer 1975a)	7.5-30 ppt		LM; Sawyer 1975b	
<i>Vannella</i> sp. A1	Schulz et al. 2015			Ca. 41.27008N, 13.0375E, surface seawater, Lago di Sabaudia, Tyrrhenian Sea coast, Latina (Italy), 33.7 ppt			LM, EM, Seq: LC025974 (SSU rDNA) Schulz et al. 2015	
<i>Vannella</i> sp. ACN1	Dyková and Kostka 2013		CC ACN1	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain			LM, EM: Dyková and Kostka 2013 Seq: JQ271724 (SSU rDNA) Dyková and Kostka 2013	
<i>Vannella</i> sp. AFSM6	Dyková et al. 2005a	Smirnov et al. 2007 (originally <i>Platyamoeba</i> sp.)	CC AFSM6	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain			LM, EM: Dyková et al. 2005a, Dyková and Kostka 2013 Seq: AY929918 (SSU rDNA), AY929934 (ITS) Dyková et al. 2005a	
<i>Vannella</i> sp. ASL3	Dyková and Kostka 2013		CC ASL3	Ca. 41.40092S, 147.12314E, gills of the cultured Atlantic salmon <i>Salmo salar</i> , Launceston School of Aquaculture, University of Tasmania, Australia			LM, EM: Dyková and Kostka 2013 Seq: JQ271725 (SSU rDNA) Dyková and Kostka 2013	
<i>Vannella</i> sp. BAK1	Dyková and Kostka 2013		CC BAK1	Ca. 1.71769N, 110.44392E, mangrove mud in Bako National Park, Sarawak, Borneo (Malaysia)			LM, EM: Dyková and Kostka 2013 Seq: JQ271726 (SSU rDNA) Dyková and Kostka 2013	
<i>Vannella</i> sp. CHOR	Dyková and Kostka 2013		CC CHOR	Decomposing crab on beach in Istria, Adriatic Sea (Croatia)			LM, EM, Seq: JQ271730 (SSU rDNA) Dyková and Kostka 2013	
<i>Vannella</i> sp. DB282	Dyková et al. 2005a	Smirnov et al. 2007 (originally <i>Platyamoeba</i> sp.)	CC DB282	Presumably east of Atlantic Ocean (Portugal), contaminant of <i>Neoparamoeba aestuarina</i> CCAP 1560/7			LM, EM: Dyková et al. 2005a, Dyková and Kostka 2013 Seq: AY929920 (SSU rDNA), AY929936 (ITS) Dyková et al. 2005a	
<i>Vannella</i> sp. ECH30	Dyková and Kostka 2013		CC ECH30	Ca. 43.28517N, 16.87264E, coelomic fluid of a purple sea urchin, <i>Sphaerechinus granularis</i> off the Brač Island, Adriatic Sea (Croatia)			LM, EM, Seq: JQ271731 (SSU rDNA) Dyková and Kostka 2013	
<i>Vannella</i> sp. ELH1-ELH7	Dyková and Kostka 2013		CC ELH1, ELH2, ELH3, ELH4, ELH5, ELH6, ELH7	Ca. 27.78634N, 18.00911W, surface of algae, beach at La Maceta, El Hierro, Canary Islands (Spain)			LM, EM, Seq: JQ271732- JQ271738 (SSU rDNA) Dyková and Kostka 2013	

Table 14. Continuation.

Vannella.sp. ISCRH	Dyková and Kostka 2013		CC ISCRH	Ca. 28.21234N, 17.2951W, sand on a beach at La Gomera, Canary Islands (Spain)		LM, EM, Seq: JQ271739 (SSU rDNA) Dyková and Kostka 2013
Vannella.sp. ISO13 ISO4 ISOKONT	Dyková and Kostka 2013, Dyková et al. 2005a		CC ISO13 ISO4 ISOKONT	Gills of a European seabass <i>Dicentrarchus labrax</i> farmed in Sicily (Italy)		LM, EM (ISO13): Dyková et al. 2005a LM, EM (ISO4, ISOKONT): Dyková and Kostka 2013 Seq: AY929905 (SSU rDNA), AY929925 (ITS) Dyková et al. 2005a, JQ271740, JQ271741 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. JKZ	Dyková and Kostka 2013		CC JKZ	Marine sand, Jeju Island, South Korea		GenBank Acc. LM, EM, Seq: JQ271243 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. KONT2Pe	Dyková and Kostka 2013		CC KONT2Pe	Contaminant of <i>Paramoeba eilhardi</i> CCAP 1560/2, presumably ca. 43.69604N, 7.30734E, algal material from The Bay of Villefranche (France)		LM, EM, Seq: JQ271245 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. LITHOV	Dyková and Kostka 2013		CC LITHOV	Material on the surface of red alga <i>Lithophyllum racemosum</i> off the Brač Island, Adriatic Sea (Croatia)		LM, EM, Seq: JQ271746 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. MSPE	Dyková and Kostka 2013		CC MSPE	Ca. 41.40092S, 147.12314E, gills of the cultivated Atlantic salmon (<i>Salmo salar</i>) used in AGD experiments, Launceston School of Aquaculture, University of Tasmania (Australia)		LM, EM, Seq: JQ271747 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. PHILM	Dyková and Kostka 2013		CC PHILM	Ca. 41.40092S, 147.12314E, gills of the cultivated Atlantic salmon (<i>Salmo salar</i>) used in AGD experiments, Launceston School of Aquaculture, University of Tasmania (Australia)		LM, EM, Seq: JQ271748 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. PHILV	Dyková and Kostka 2013		CC PHILV	Ca. 42.17405S, 145.31038E, gills of Atlantic salmon <i>Salmo salar</i> , Maquarie Harbour, Tasmania (Australia)		LM, EM, Seq: JQ271749 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. PMCH	Dyková et al. 2005a	Smirnov et al. 2007 (originally <i>Platyamoeba</i> sp.)	CC PMCH	Ca. 44.85955N, 13.8215E, coelomic fluid of the marbled rock crab, <i>Pachygrapsus marmoratus</i> , beach in Pula, Adriatic Sea (Croatia)		LM, EM, Seq: AY929919 (SSU rDNA), AY929935 (ITS) Dyková et al. 2005a, Dyková and Kostka 2013
Vannella sp. R	Dyková and Kostka 2013		CC R	Ca. 30.37854N, 88.81847W, haemolymph of blue crab, <i>Callinectes sapidus</i> , Gulf of Mexico coast, Mississippi (USA)		LM, EM, Seq: JQ271750 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. RSSF	Dyková and Kostka 2013		CC RSSF	Ca. 41.40092S, 147.12314E, gills of the cultivated Atlantic salmon (<i>Salmo salar</i>) used in AGD experiments, Launceston School of Aquaculture, University of Tasmania (Australia)		LM, EM, Seq: JQ271752 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. S2M2	Dyková et al. 2005a		CC S2M2	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain		LM, EM, Seq: AY929904 (SSU rDNA), AY929924 (ITS) Dyková et al. 2005a, Dyková and Kostka 2013
Vannella sp. S3M13	Dyková and Kostka 2013		CC S3M13	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain		LM, EM, Seq: JQ271754 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. S4M23	Dyková and Kostka 2013		CC S4M23	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain		LM, EM, Seq: JQ271755 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. S4M24	Dyková and Kostka 2013		CC S4M24	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain		LM, EM, Seq: JQ271756 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. S4M30	Dyková and Kostka 2013		CC S4M30	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain		LM, EM, Seq: JQ271757 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. S6M33	Dyková and Kostka 2013		CC S6M33	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain		LM, EM, Seq: JQ271758 (SSU rDNA) Dyková and Kostka 2013

Table 14. Continuation.

Vannella sp. S7M35	Dyková and Kostka 2013		CC S7M35	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain	LM, EM, Seq: JQ271759 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. S7M36	Dyková and Kostka 2013		CC S7M36	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain	LM, EM, Seq: JQ271760 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. S98M54F	Dyková and Kostka 2013		CC S98M54F	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain	LM, EM, Seq: JQ271761 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. S98M55	Dyková et al. 2005a		CC S98M55	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain	LM, EM, Seq: AY929907 (SSU rDNA), AY929927 (ITS) Dyková et al. 2005a, Dyková and Kostka 2013
Vannella sp. S98M7	Dyková and Kostka 2013		CC S98M7	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain	LM, EM, Seq: JQ271762 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. S98M8	Dyková et al. 2005a		CC S98M8	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain	LM, EM, Seq: AY929906 (SSU rDNA), AY929926 (ITS) Dyková et al. 2005a, Dyková and Kostka 2013
Vannella sp. SBV1	Dyková et al. 2005a	Smirnov et al. 2007 (originally <i>Platyamoeba</i> sp.)	CC SBV1	Gas bladder content of a European seabass <i>Dicentrarchus labrax</i> farmed in Sicily (Italy)	LM, EM, Seq: AY929917 (SSU rDNA), AY929933 (ITS) Dyková et al. 2005a, Dyková and Kostka 2013
Vannella sp. SEDFS	Dyková and Kostka 2013		CC SEDFS	Ca. 43.33871S, 147.02928E, sediment under the Salmo salar sea cage, Stringers Cove, Tasmania (Australia)	LM, EM, Seq: JQ271763 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. SMA13V	Dyková and Kostka 2013		CC SMA13V	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain	LM, EM, Seq: JQ271764 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. SMA26	Dyková and Kostka 2013		CC SMA26	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain	LM, EM, Seq: JQ271765 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. SMA30	Dyková and Kostka 2013		CC SMA30	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain	LM, EM, Seq: JQ271766 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. SMA7V	Dyková and Kostka 2013		CC SMA7V	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain	LM, EM, Seq: JQ271767 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. SS8FJ1	Dyková et al. 2005a		CC SS8FJ1	Gills of Atlantic salmon, <i>Salmo salar</i> , farmed in Farad (Ireland)	LM, EM, Seq: AY929915 (SSU rDNA), AY929931 (ITS) Dyková et al. 2005a, Dyková and Kostka 2013
Vannella sp. SYM43	Dyková and Kostka 2013		CC SYM43	Gills of turbot, <i>Scophthalmus maximus</i> farmed in North-Western Spain	LM, EM, Seq: JQ271768 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. T02	Dyková and Kostka 2013		CC T02	Ca. 34.71106S, 135.86313E, gills of a dead Southern Bluefin tuna (<i>Thunnus maccoyii</i>), Port Lincoln, (Australia)	LM, EM, Seq: JQ271769 (SSU rDNA) Dyková and Kostka 2013
Vannella sp. ULLAP	Dyková and Kostka 2013			Ca. 57.89349N, 5.16429W, marine sand, beach at Ullapool, Scotland (UK)	LM, EM, Seq: JQ271770 (SSU rDNA) Dyková and Kostka 2013

Table 15. *Discosea*, *Stygamoebida*.

Species	Initial description	Redescription and earlier synonyms (if present)	Strains if available	Habitat	Salinity tolerance range if available	Data available
<i>Stygamoeba Sawyer, 1975.</i>						
<i>Stygamoeba cauta</i>	Lotonin and Smirnov 2020			55.92054N, 12.52338E, upper layer of sediments (sand, anaerobic bacterial mats), Nivå Bay, The Sound, Denmark; 1.5 ppt		LM: Lotonin and Smirnov 2020 Seq: MN547354 - MN547356 (SSU rDNA), Lotonin and Smirnov 2020
<i>S. polymorpha</i>	Sawyer 1975a			Seawater, Chincoteague Bay near Greenbacksville, Virginia, US; 28.9-30.7 ppt (Sawyer 1975a)	7.5-30 ppt (Sawyer 1975a)	LM: Sawyer 1975a
<i>S. regulata</i>	Smirnov 1995		CCAP 1580/1(T+) ATCC 50892 (Lahr et al. 2011)	CCAP 1580/1: 55.92054N, 12.52338E; upper layer of sediments (sand, anaerobic bacterial mats), Nivå Bay, The Sound (Denmark), 15 ppt (Smirnov 1995) ATCC 50892: ca. 37.26598N, 76.38467W; salt marsh bottom sediments, Hog Island, Virginia, US	15-35 ppt (Smirnov 1995)	LM: Smirnov 1995, Lahr et al. 2011 EM: Smirnov 1995 Seq: JF694285, MN547357 (SSU rDNA), Lahr et al. 2011; Lotonin and Smirnov 2020 JF694322 (actin) Lahr et al. 2011 Tr: SAMN02740477 (Keeling et al. 2014)
<i>Vermistella Moran et al. 2007.</i>						
<i>Vermistella antarctica</i>	Moran et al. 2007		ATCC PRA-216(T)	76.88333S, 154.23333W, bottom sediment near the Ross Ice Shelf, Antarctica; depth 290 m (Moran et al. 2007)		LM, EM: Moran et al. 2007 Seq: DQ229956 (SSU rDNA), Moran et al. 2007
<i>V. arctica</i>	Tyml et al. 2016		DX2: CCAP 2581/1; DC17C: CCAP 2581/2; SV198: CCAP 2581/3(T) (none of the strains is visible in CCAP catalogue)	Strain DX2: body surface of the tubeworm <i>Circeis spirillum</i> , 78°40'N, 16°28'E, Petuniabukta, Billenfjorden, Svalbard Archipelago; depth 10-20 m; temperature +4°C; July 2012 Strain DC17C: body surface of the tubeworm <i>Circeis spirillum</i> , 78°39'N, 16°42'E, Brucebyen, Billenfjorden, Svalbard Archipelago; depth 10-20 m; temperature +4°C; July 2012 Strain SV198: gills of the hermit crab <i>Pagurus pubescens</i> , 78°31'N, 16°4'E, Skansbukta, Billenfjorden, Svalbard Archipelago; depth 10-20 m; temperature +4°C; August 2009 (Tyml et al. 2016)		LM, EM: Tyml et al. 2016 Seq: KJ874207 - KJ874209 (SSU rDNA), KJ874216 - KJ874227 (actin), Tyml et al. 2016

Table 16. Discosea, Centramoebia, Acanthopodida.

Species	Initial description	Redescription and earlier synonyms (if present)	Strains if available	Habitat	Salinity tolerance range if available	Data available
Acanthamoeba Volkonsky, 1930.						
<i>A. gigantea</i>	Schmoller 1964			Ca. 54.17699N, 12.05022E, green algae at the upper littoral, Baltic Sea, Germany		LM: Schmoller 1964
<i>A. griffini</i>	Sawyer 1971b		ATCC 30731(T), ATCC 50702 CCAP 1501/4(T)	Ca. 41.32827N, 72.09108W, sandy beach opposite Pequot Avenue, New London, Connecticut (US), 24–28 ppt; Sawyer 1971b	0–32 ppt (Sawyer 1971b)	LM: Sawyer 1971b, Page 1983a Seq: U02540 (SSU rDNA group I intron) Gast et al. 1994, U07412 (SSU rDNA) Gast et al. 1996, S81337 (SSU rDNA) Ledee et al. 1996, AF239295 (SSU rDNA) Khan et al. 2002, AF479562 (16S rDNA) Ledee et al. 2003, GU553135, GU597016–GU597017, (SSU rDNA) Hsu et al., unpublished, HQ007040 (SSU rDNA) Garcia et al. 2011, KC694190–KC694191 (SSU rDNA) Ghasemi et al., unpublished, KF010846 (SSU rDNA) Heredero–Bermejo et al. 2015, KF914142 (SSU rDNA) Gonzalez-Robles et al. 2014, KJ446979–KJ446980 (SSU rDNA) Eyyapan et al., unpublished, KR872643–KR872644 (SSU rDNA) Koltas et al. 2015, KU175890, KU759839 (SSU rDNA), MF563609 (16S rDNA) Megha et al., unpublished, KY072279 (SSU rDNA) Martin-Perez et al. 2017, KY488310–KY488312 (SSU rDNA) Solhoo et al., unpublished, MF100899 (SSU rDNA) Basher et al. 2017, MG945004 (SSU rDNA) Degerli et al., unpublished, MZ314026 (SSU rDNA) Karyagdi et al., unpublished, LM: Sawyer et al. 1977
<i>A. hatchetti</i>	Sawyer et al. 1977			Ca. 39.18233N, 76.44718W, brackish-water sediments, Brewerton Channel, Baltimore, Maryland (US)		LM: Sawyer et al. 1977 Seq: AF019060 (designated ATCC 30731 in GenBank) AF019068 (SSU rDNA) Stothard et al. 1998, AF251937, AF251939 (SSU rDNA) Walochnik et al. 2000a, AF260722–AF260723 (SSU rDNA) Walochnik et al. 2000b, AF526425–AF526428 (ITS1) Koehlsler et al., unpublished, DQ152194–DQ152195 (subtilisin-like serine proteinase gene) Blaschitz et al. 2006, JF508857 (SSU rDNA) Conza, unpublished, KCL164222, KCL164235, KC346960 (SSU rDNA) Conza et al., unpublished, KJ801938 (SSU rDNA) Begg et al. 2014, KX675340–KX675341, KX709491–KX709495 (SSU rDNA), MF563610 (16S rDNA) Megha et al., unpublished, KY072778 (SSU rDNA) Martin-Perez et al. 2017, KY934459 (SSU rDNA) Corsaro et al. 2018, MG945012–MG945014 (SSU rDNA) Degerli et al., unpublished, MH124181–MH124183, MH124197 (COI), MN129723, MN129725, MN129743, MN129747 (ND5) Kohlsler et al., unpublished, MH790988–MH790989, MH790999, MH791025, MN700275, MN700300, MN700303–MN700304 (SSU rDNA) Rosnani Hanim et al., unpublished, MK713905, MK713909, MK713927 (SSU rDNA) Roshni Swasthikka et al., unpublished, MK905437 (SSU rDNA) Milanez et al. 2020, MT226327 (SSU rDNA) Milanez et al., unpublished, MT261771 (SSU rDNA) Paes and Rott, unpublished, MW350039 (SSU rDNA) Masangkay et al., unpublished, MZ504292 (SSU rDNA) El-Wakil et al., unpublished.
Protacanthamoeba Page, 1981.						
<i>Protacanthamoeba caledonica</i>	Page 1981a			River Morar estuary, Westrn Scotland (UK), brackish water.		LM, EM: Page 1981a

Table 17. Discosea, Centramoebia, Himatimena. *Discosea*, *Centramoebia*, *Himatimena*.

Species	Initial description	Redescription and earlier synonyms (if present)	Strains if available	Habitat	Salinity tolerance range if available	Data available
<i>Parvamoeba</i> Rogerson, 1993.						
<i>Parvamoeba rugata</i>	Rogerson 1993		CCAP 1556/1(T)	Ca. <i>Fucus serratus</i> surface washings at the intertidal zone, Marine station Millport, Cumbrae Island, UK; 30 ppt		LM, EM: Rogerson 1993; Kudryavtsev 2012 Seq: JN202427-IN202433 (SSU rDNA), JN202434-IN202435 (COI) Kudryavtsev 2012, MT975637-MT975642 (actin) Kudryavtsev et al. 2021
<i>Parvamoeba monaura</i>	Cole et al. 2010		ATCC PRA-35(T)	41.02501N, 73.36541W, <i>Homarus americanus</i> carapace surface, Long Island Sound near Oyster Bay, New York, US	10-30 ppt	LM, EM: Cole et al. 2010 Seq: EF455775 (SSU rDNA), EF455789 (β-tubulin), EF455756 (α-tubulin), EF455773 (actin); Cole et al. 2010
<i>Ovalopodium</i> Sawyer, 1980.						
<i>Ovalopodium carrikeri</i>	Sawyer 1980			Ca. 38.79157N, 75.15954W; University of Delaware mariculture facility, Lewes, Delaware (US)		LM: Sawyer 1980
<i>O. rosalinum</i> Völcker and Kudryavtsev, 2021	Kudryavtsev et al. 2021			Ca. 53.748333N, 7.479717E; co-culture with the foraminiferan <i>Rosalina</i> sp., collected in 1984 from the beach at Langeoog Island (Frisian Islands, North Sea, Germany); 30 ppt		LM, EM: Kudryavtsev et al. 2021 Seq: MT975614-MT975618 (SSU rDNA), MW026146-MW026150 (actin), MT975622-MT975624 (COI); Kudryavtsev et al. 2021
<i>Planopodium</i> Völcker and Kudryavtsev, 2021.						
<i>Planopodium desertum</i>	Kudryavtsev et al. 2011b	Kudryavtsev et al. 2021; <i>Ovalopodium desertum</i> (Kudryavtsev et al. 2011b)	CCAP 1530/1(T)	Ca. 43.5N, 77.0E; bottom sediments in the littoral zone, semidesert pond in the south of Kazakhstan (Central Asia); 3-4 ppt		LM, EM: Kudryavtsev et al. 2011b Seq: JF298243-JF298247 (SSU rDNA), JF298258 (actin); Kudryavtsev et al. 2011b, MT975627 (COI); Kudryavtsev et al. 2021 Ti: PRJNA222682 (Cavalier-Smith et al. 2015)
<i>Cochliopodium</i> Hertwig and Lesser, 1874.						
<i>Cochliopodium clarum</i>	Schaeffer 1926		ATCC 30975 (Sawyer 1971)	Marine tidal pool with diatoms and other algae, Cold Spring Harbor, Long Island, US (Schaeffer 1926); ca. 38.66996N, 76.18194W; seawater, Tred Avon River, Chesapeake Bay, Maryland, US; 9-16 ppt (ATCC 30975; Sawyer 1971); (data in ATCC database on strain ATCC 30975 provide "seawater holding tank, Northeast Fisheries Center, Oxford, Maryland, US" which geographically fits Sawyer's isolation site)	0-30 ppt (Sawyer 1971; Schaeffer 1926)	LM: Schaeffer 1926; Sawyer 1971
<i>C. gallicum</i>	Kudryavtsev and Smirnov 2006		CCAP 1537/6	Saline pool with artificial bacterial mats in the Camargue Natural Reserve, Mediterranean Sea, France; 40-42 ppt	At least up to 60 ppt (Kudryavtsev and Smirnov 2006)	LM, EM: Kudryavtsev and Smirnov 2006 Seq: MT975609-MT975613 (SSU rDNA), MT975592-MT975595 (actin), KJ781467, KJ781468, MT975630 (COI), Kudryavtsev et al. 2021; Tekle 2014
<i>C. gulosum</i>	Schaeffer 1926			<i>Zostera</i> sp. and other submerged sea-weeds, Cold Spring Harbor, Great South Bay, Long Island, US (Schaeffer 1926); 66.30623N, 33.64762E, sand from the intertidal zone of the Keret Island (Chupa Inlet, Kandalaksha Bay, the White Sea, NW Russia); 15-17 ppt (Kudryavtsev 1999, 2000)		LM: Schaeffer 1926, Kudryavtsev 1999 EM: Kudryavtsev 2000
<i>C. maeoticum</i>	Kudryavtsev 2006			Ca. 47.25322N, 39.04674E; bottom sediments from the Gulf of Taganrog (the Azov Sea, Russia); ca. 2.5 ppt		LM, EM: Kudryavtsev 2006
<i>C. radiosum</i>	Biernacka 1963			Ca. 54.4051N, 18.83246E, Bay of Gdansk, Baltic Sea (Poland), 6.5-7.5 ppt		LM: Biernacka 1963
<i>C. spiniferum</i>	Kudryavtsev 2004		CCAP 1537/3	66.28514N, 33.63965E; bottom sediments of a stream flowing through a periodically flooded marsh near the Marine Biological Station of the St. Petersburg University at Srednii Island (Chupa Inlet, Kandalaksha Bay, the White Sea), freshwater-15 ppt, 6 ppt at the moment of sampling		LM, EM: Kudryavtsev 2004 Seq: AY775130 (SSU rDNA), JF298273-JF298279 (actin), KJ781455-KJ781459, MT975625 (COI), Kudryavtsev et al. 2005, 2011b, 2021; Tekle 2014

Table 18. Discosea, Centramoebia, Pellitida.

Species	Initial description	Redescription and synonyms (if present)	Strains if available	Habitat	Salinity tolerance range if available	Data available
<i>Pellita Smirnov and Kudryavtsev, 2005</i>	Smirnov and Kudryavtsev 2005		ATCC PRA-25	Ca. 40.70003N, 0.84762E, stratified cyanobacterial mats in the system of natural channels: Ebro River delta, Spain; salinity 70–80 ppt; depth 0.2–0.3 m (Smirnov and Kudryavtsev 2005) 55.92054N, 12.52338E: upper layer of sediments (sand, anaerobic bacterial mats), Nivå Bay, The Sound, Denmark; 15 ppt (Smirnov and Kudryavtsev 2005) ATCC PRA-25: 41.02501N, 73.36541W, carapax surface of female <i>Homarus americanus</i> , collected off the coast of Norwalk, Connecticut, US (Kudryavtsev et al. 2014)		LM, EM: Smirnov and Kudryavtsev 2005; Kudryavtsev et al. 2014 Seq: KF705039 (SSU rDNA), Kudryavtsev et al. 2014

These cases may be due to the stability of cysts in the seawater (Page, 1983a). Despite morphological identities to previously described species, one should bear in mind the possibilities of cryptic speciation as shown earlier in some other amoebozoans (Kudryavtsev and Volkova, 2020). We list here only those species initially described from marine or brackish water biotopes.

Discosea, Centramoebia, Himatistenida (Table 17).

Parvamoeba Rogerson, 1993. This genus is one of the smallest in Amoebozoa, and includes two marine species discovered in the last decades. This may be due to their small size, while the actual diversity may be larger. The type species of this genus was provisionally included in the Thecamoebidae based on morphology (Rogerson, 1993), but further detailed studies, including gene sequence analysis placed *Parvamoeba* in Himatistenida (Cole et al., 2010; Kudryavtsev, 2012; Kudryavtsev et al., 2021).

Ovalopodium Sawyer, 1980. This is an elusive genus, because its type species has never been reisolated with certainty since its initial description. Hence, it has only light microscopic images available. Because of this, a species that was added to this genus in 2011 (Kudryavtsev et al., 2011b) had to be transferred into *Planopodium* (Kudryavtsev et al., 2021) after it became clear that there was a higher diversity of small deeply-branching himatistenid lineages than estimated before.

Planopodium Völcker and Kudryavtsev, 2021. This genus comprises two species, of which one, *P. desertum* (Kudryavtsev et al., 2011), was isolated from a very weakly saline continental pond in an arid area, and initially included in *Ovalopodium*, while another species is freshwater. These species are different morphologically, but almost identical in gene sequence data (Kudryavtsev et al., 2021).

Cochliopodium Hertwig and Lesser, 1874. This genus with about 20 named species is known for almost 150 years already, but most of its species are from fresh water and soil. The first two marine species of this genus were described only by Schaeffer (1926). Only two named marine species have gene sequence data available.

Discosea, Centramoebia, Pellitida (Table 18).

Pellita Smirnov and Kudryavtsev, 2005. Pellitida were established only recently (Smirnov and Kudryavtsev, 2005; Smirnov et al., 2011), although some

Table 19. Amoebozoa incertae sedis.

Species	Initial description	Redescription and synonyms (if present)	Strains if available	Habitat	Salinity tolerance range if available	Data available
<i>Belonocystis marina</i>	Klimov and Ziatogursky 2016		CCM 00448	66.31143N, 33.63858E, seawater from salt marsh near Matryomyn Island, Chupa Inlet, Kandalaksha Bay, the White Sea (Russia), 16 ppt	10-60 ppt	LM, EM: Klimov and Ziatogursky 2016
<i>Boveella obscura</i>	Sawyer 1975a			Surface seawater of Chincoteague Bay near Greenbackville, Virginia (US), 25.7-28.9 ppt		LM: Sawyer 1975a
<i>Corallomyxa chattoni</i>	Grell and Benwitz 1978	Possible earlier synonym: <i>Cinetidomyxa chattoni</i> (Cachon and Cahon-Enjumeat 1965; Grell and Benwitz 1978)		Ca. 43.69604N, 7.30734E, marine algae near Villefranche-sur-mer Marine Station, Mediterranean Sea, France		LM, EM: Grell and Benwitz 1978
<i>C. multipara</i>	Grell 1988			Ca. 19.27419S, 147.04788E, fallen leaves of mangroves in seawater, littoral, near Australian Institute of Marine Science, Townsville, Queensland, Australia		LM: Grell 1988
<i>C. mutabilis</i>	Grell 1966			Ca. 13.40742S, 48.29215E, dead coral reef blocks, Nosy Be oceanography Station (now National Centre for Oceanography Research), Nosy-Be Island, Madagascar; Ca. 23.37253S, 43.65754E, dead coral reef blocks, Marine Station Tuléar (now Institute of Fisheries and Marine Science), Tuléar, Madagascar		LM: Grell 1966 EM: Grell and Benwitz 1978
<i>C. nipponica</i>	Grell 1991			Ca. 34.66681N, 138.93621E, bottom sediment, tidal pools near the Shimoda Marine Research Center, Shimoda, Japan		LM, SEM: Grell 1991
<i>Gibbidiscus gemma</i>	Schaeffer 1926			Seawater tank, Tortugas Marine Laboratory, Florida (US); seawater in tidal pool, Sand Key, Tortugas, Florida (US)		LM: Schaeffer 1926
<i>G. newmani</i>	Sawyer 1975b			Marine surface water, Chincoteague Bay, Virginia (US), 30.2 ppt	3-30 ppt (survival) 7.5-30 ppt (growth)	LM: Sawyer 1975b
<i>Rhabdamoeba marina</i>	Dunkerly 1921			Marine material associated with <i>Trichosphaerium</i> sp. From the Marine Laboratory, Plymouth (UK) (Dunkerly 1921) Ca. 55.75157N, 4.92456W, benthic sand, depth 10 m, Newtown Bay, Firth of Clyde, Scotland (UK) (Rogerson et al. 1998)		LM: Dunkerly 1921, Rogerson et al. 1998 EM: Rogerson et al. 1998
<i>Stereomyxa angulosa</i>	Grell 1966			Ca. 13.40742S, 48.29215E, dead coral reef blocks, Nosy Be oceanography Station (now National Centre for Oceanography Research), Nosy-Be Island, Madagascar; Ca. 23.37253S, 43.65754E, dead coral reef blocks, Marine Station Tuléar (now Institute of Fisheries and Marine Science), Tuléar, Madagascar		LM: Grell 1966 EM: Benwitz and Grell 1971a
<i>S. ramosa</i>	Grell 1966			Ca. 13.40742S, 48.29215E, dead coral reef blocks, Nosy Be oceanography Station (now National Centre for Oceanography Research), Nosy-Be Island, Madagascar; Ca. 23.37253S, 43.65754E, dead coral reef blocks, Marine Station Tuléar (now Institute of Fisheries and Marine Science), Tuléar, Madagascar		LM: Grell 1966 EM: Benwitz and Grell 1971b
<i>Strioliatus* tardus</i>	Schaeffer 1926			Seawater among blue-green algae, Key West, Florida (US)	9-35 ppt	LM: Schaeffer 1926
<i>Trienamoeba jachowskii</i>	Sawyer 1975a			Marine surface water, Chincoteague Bay, Virginia (US), 29-29.5 ppt	7.5-30 (survival), growth	LM: Sawyer 1975a

Table 19. Continuation.

Unda maris	Schaeffer 1926			Seawater tank, Tortugas Marine Laboratory, Florida (US)	3.5-35 ppt (survival)	LM: Schaeffer 1926
Unda schaefferi	Sawyer 1975b	ATCC 50810 (strain isolated by T.K. Sawyer in 1999)		Marine surface water, Chincoteague Bay, Virginia (US), 30.2 ppt (Sawyer 1975b), 37.44458N, 75.84187W, sediment core from Red Bank at University of Virginia LTER site (ATCC 50810; isolated by T.K. Sawyer in 1999)	15-30 ppt (survival and growth)	LM: Sawyer 1975b Tr: PRJNA316021 (Tekle et al. 2016)

* This genus is not listed in the paper by Adl et al. (2019), although to our knowledge it was never invalidated.

members of this clade were known for a long time, like *Gocevia* Valkanov, 1932 and *Endostelium* Olive et al., 1984. Only one marine species of *Pellita* was isolated several times from different biotopes.

Amoebozoa incertae sedis (Table 19).

***Belonocystis* Rainer, 1968, *Boveella* Sawyer, 1975, *Corallomyxa* Grell, 1966, *Gibbodiscus* Schaeffer, 1926, *Rhabdamoeba* Dunkerly, 1921, *Stereomyxa* Grell, 1966, *Striolatus* Schaeffer, 1926, *Triaenamoeba* Bovee, 1953, *Unda* Schaeffer, 1926.** The listed genera are either monotypic or comprise up to four species. All of them are marine, except for *Belonocystis* that also comprises freshwater species. For none of them molecular data are available, therefore, their position in the system is still incertae sedis. One exception is *Unda*, for which a transcriptome was sequenced (Tekle et al. 2016), however, the generic identity of the sequenced strain is unclear.

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References

Adl S.M., Bass D., Lane C.E., Lukeš J., Schoch C.L., Smirnov A. et al. 2019. Revisions to the classification, nomenclature, and diversity of eukaryotes. *J. Eukaryot. Microbiol.* 66, 4–119. <https://doi.org/10.1111/jeu.12691>

Amaral Zettler L.A., Nerad T.A., O’Kelly C.J., Peglar M.T., Gillevet P.M., Silberman J.D. et al. 2000. A molecular reassessment of the leptomyxid amoebae. *Protist.* 151, 275–282. <https://doi.org/10.1078/1434-4610-00025>

Anderson O.R. 1994. Fine structure of the marine amoeba *Vexillifera telmathalassa* collected from

a coastal site near Barbados with a description of salinity tolerance, feeding behavior and prey. *J. Eukaryot. Microbiol.* 41, 124–128. <https://doi.org/10.1111/j.1550-7408.1994.tb01484.x>

Anderson O. R. and Rogerson A. 1995. Annual abundances and growth potential of gymnamoebae in the Hudson Estuary with comparative data from the Firth of Clyde. *Eur. J. Protistol.* 31, 223–233. [https://doi.org/10.1016/S0932-4739\(11\)80446-3](https://doi.org/10.1016/S0932-4739(11)80446-3)

Anderson O.R., Rogerson A. and Hannah F. 1997. Three new limax amoebae isolated from marine surface sediments: *Vahlkampfia caledonica* N. Sp., *Saccamoeba marina* N. Sp., and *Hartmannella vacuolata* N. Sp. *J. Eukaryot. Microbiol.* 44, 33–42. <https://doi.org/10.1111/j.1550-7408.1997.tb05688.x>

Anderson O.R., Nerad T.A. and Cole J.C. 2003. *Platyamoeba nucleolilateralis* n. sp. from the Chesapeake Bay Region. *J. Eukaryot. Microbiol.* 50, 57–60. <https://doi.org/10.1111/j.1550-7408.2003.tb00106.x>

Angell R.W. 1975. Structure of *Trichosphaerium micrum* sp. n. *J. Protozool.* 22, 18–22. <https://doi.org/10.1111/j.1550-7408.1975.tb00937.x>

Angell R.W. 1976. Observations on *Trichosphaerium platyxyrum* sp. n. *J. Protozool.* 23, 357–364. <https://doi.org/10.1111/j.1550-7408.1976.tb03788.x>

Bark A. W. 1973. A study of the genus *Cochliopodium* Hertwig and Lesser 1874. *Protistologica.* 9, 119–138.

Basher M.H.A., Ithoi I., Mahmud R., Abdulsalam A.M., Foad A.I., Dawaki S. et al. 2017. Occurrence of *Acanthamoeba* genotypes in Central West Malaysian environments. *Acta Trop.* 178, 219–228. <https://doi.org/10.1016/j.actatropica.2017.11.015>

Begg A.P., Todhunter K., Donahoe S.L., Krockenberger M. and Slapeta J. 2014. Severe amoebic placentitis in a horse caused by an *Acanthamoeba hatchetti* isolate identified using next-generation sequencing. *J. Clin. Microbiol.* 52, 3101–3104. <https://doi.org/10.1128/JCM.01071-14>

Benwitz G. and Grell K.G. 1971a. Ultrastruktur mariner Amöben. II. *Stereomyxa ramosa*. *Arch. Protistenkd.* 113, 51–67.

Benwitz G. and Grell K. G. 1971b. Ultrastruktur mariner Amöben. III. *Stereomyxa angulosa*. *Arch. Protistenkd.* 113, 68–79.

Biernacka I. 1963. Die Protozoenfauna in Danziger Bucht. *Pol. Arch. Hydrobiol.* 11, 17–75.

Blaschitz M., Kohsler M., Aspöck H. and Walochnik J. 2006. Detection of a serine proteinase

gene in *Acanthamoeba* genotype T6 (Amoebozoa: Lobosea). *Exp. Parasitol.* 114, 26–33. <https://doi.org/10.1016/j.exppara.2006.02.004>

Boenigk J., Ereshefsky M., Hoef-Emden K., Mallet J. and Bass D. 2012. Concepts in protistology: Species definitions and boundaries. *Eur. J. Protistol.* 48, 96–102. <https://doi.org/10.1016/j.ejop.2011.11.004>

Bolivar I., Fahrni J. F., Smirnov A. and Pawlowski J. 2001. SSU rRNA-based phylogenetic position of the genera *Amoeba* and *Chaos* (Lobosea, Gymnamoebia): the origin of gymnamoebae revisited. *Mol. Biol. Evol.* 18, 2306–2314. <https://doi.org/10.1093/oxfordjournals.molbev.a003777>

Bondarenko N.I., Bondarenko A.S. and Smirnov A.V. 2017. Lineage-specific and highly derived gene sequences among amoebozoa, revealed by the comparative analysis of transcriptomes from twelve amoebozoan species. *J. Eukaryot. Microbiol.* 64, 622–631. <https://doi.org/10.1111/jeu.12397>

Bovee E.C. 1956a. Some observations on the morphology and activities of a new ameba from citrus wastes, *Flamella citrensis* n. sp. *J. Protozool.* 3, 151–155. <https://doi.org/10.1111/j.1550-7408.1956.tb02450.x>

Bovee E.C. 1956b. Some observations on a marine ameba of intertidal zones, *Vexillifera telmathalassa*, n. sp. *J. Protozool.* 3, 155–158. <https://doi.org/10.1111/j.1550-7408.1956.tb02451.x>

Bovee E.C. 1965. An emendation of the ameba genus *Flabellula* and a description of *Vannella* gen. nov. *Trans. Amer. Microsc. Soc.* 84, 217–227. <https://doi.org/10.2307/3224288>

Bovee E.C. 1985. The lobose amebas III. Descriptions of nine new conopodous amebas of the genus *Vexillifera* Schaeffer, 1926, emd. Bovee 1951, 1970, with comments on the genus. *Arch. Protistenkd.* 129, 101–118. [https://doi.org/10.1016/S0003-9365\(85\)80013-0](https://doi.org/10.1016/S0003-9365(85)80013-0)

Bovee E.C. and Jahn T.L. 1965. Mechanisms of movement in taxonomy of Sarcodina. II. The organization of subclasses and orders in relationship to the classes Autotractea and Hydraulea. *Am. Midl. Nat.* 73, 293–298. <https://doi.org/10.2307/2423456>

Bovee E.C. and Jahn T.L. 1966. Mechanisms of movement in taxonomy or sarcodina. III. Orders, suborders, families, and subfamilies in the superorder Lobida. *Syst. Zool.* 15, 229–240. <https://doi.org/10.2307/sysbio/15.3.229>

Bovee E.C. and Sawyer T.K. 1979. Marine flora and fauna of the northeastern United States.

- Protozoa: Sarcodina: Amoebae. NOAA Technical Report, Washington. <https://doi.org/10.5962/bhl.title.63225>
- Bustos P.A., Young N.D., Rozas M.A., Bohle H.M., Idefonso R.S., Morrison R.N. et al. 2011. Amoebic gill disease (AGD) in Atlantic salmon (*Salmo salar*) farmed in Chile. *Aquaculture*. 310, 281–288. <https://doi.org/10.1016/j.aquaculture.2010.11.001>
- Butler H. and Rogerson A. 1996. Growth potential, production efficiency and annual production of marine benthic naked amoebae (gymnamoebae) inhabiting sediments of the Clyde Sea area, Scotland. *Aquat. Microb. Ecol.* 10, 123–129. <https://doi.org/10.3354/ame010123>
- Butler H. and Rogerson A. 1997. Consumption rates of six species of marine benthic naked amoebae (*Gymnamoebia*) from sediments in the Clyde Sea area. *J. Mar. Biol. Assoc. UK* 77, 989–997. <https://doi.org/10.1017/S0025315400038571>
- Cachon J. and Cachon-Enjumet M. 1965. Cytologie et cycle évolutif de *Cinetidomyxa chattoni* nov. sp., Heliozoaire Proteomyxee. *Arch. Zool. Exp. Gen.* 104, 47–196.
- Calkins G.N. 1902. Marine protozoa from Woods Hole. US Government Printing Office.
- Cann J.P. and Page F.C. 1982. Fine structure of small free-living *Paramoeba* (Amoebida) and taxonomy of the genus. *J. Mar. Biol. Ass. U. K.* 62, 25–43. <https://doi.org/10.1017/S0025315400020087>
- Caraguel C.G., O’Kelly C.J., Legendre P., Frasca S., Gast R.J., Despres B.M. et al. 2007. Microheterogeneity and coevolution: An examination of rDNA sequence characteristics in *Neoparamoeba pemaquidensis* and its prokinetoplastid endosymbiont. *J. Eukaryot. Microbiol.* 54, 418–426. <https://doi.org/10.1111/j.1550-7408.2007.00281.x>
- Cash J. and Hopkinson J. 1905. The British freshwater Rhizopoda and Heliozoa. 1, The Ray Society, London. <https://doi.org/10.5962/bhl.title.927>
- Cash J. and Hopkinson, J. 1909. The British freshwater Rhizopoda and Heliozoa. 2, The Ray Society, London.
- Cavalier-Smith T., Chao E. E.-Y. and Oates B. 2004. Molecular phylogeny of Amoebozoa and the evolutionary significance of the unikont *Phalansterium*. *Eur. J. Protistol.* 40, 21–48. <https://doi.org/10.1016/j.ejop.2003.10.001>
- Cavalier-Smith T., Fiore-Donno A.M., Chao E., Kudryavtsev A., Berney C., Snell E. A. et al. 2015. Multigene phylogeny resolves deep branching of Amoebozoa. *Mol. Phylogenet. Evol.* 83, 293–304. <https://doi.org/10.1016/j.ympev.2014.08.011>
- Cavalier-Smith T., Chao E.E. and Lewis R. 2016. 187-gene phylogeny of protozoan phylum Amoebozoa reveals a new class (Cutosea) of deep-branching, ultrastructurally unique, enveloped marine Lobosa and clarifies amoeba evolution. *Mol. Phylogenet. Evol.* 99, 275–296. <https://doi.org/10.1016/j.ympev.2016.03.023>
- Cenci U., Moog D., Curtis B. A., Tanifuji G., Eme L., Lukeš J. et al. 2016. Heme pathway evolution in kinetoplastid protists. *BMC Evol. Biol.* 16, 1–18. <https://doi.org/10.1186/s12862-016-0664-6>
- Chatton E. 1953. Classe des Lobosa Leidy, 1879. Ordre des Amoebiens nus ou Amoebaea. In: *Traité de Zoologie*, 1. Masson et Cie, Paris, pp. 5–91.
- Cheng T. C. 1970. *Hartmannella tahitiensis* sp. n., an amoeba associated with mass mortalities of the oyster *Crassostrea commercialis* in Tahiti, French Polynesia. *J. Invertebr. Pathol.* 15, 405–419. [https://doi.org/10.1016/0022-2011\(70\)90185-0](https://doi.org/10.1016/0022-2011(70)90185-0)
- Chystyakova L.V., Miteva O.A. and Frolov A.O. 2012. Morphology of *Mastigamoeba aspera* Schulze, 1875 (Archamoebae, Pelobiontida). *Cell Tiss. Biol.* 6, 189–196. <https://doi.org/10.1134/S1990519X12020058>
- Cienkowski L. 1881. An account on the White Sea excursion in 1880. *Proc. St.-Petersb. Imp. Soc. Nat.* 12, 130–171 (in Russian).
- Cole J., Anderson O.R., Tekle Y.I., Grant J., Katz L.A. and Nerad T., 2010. A description of a new “amoebozoan” isolated from the American lobster *Homarus americanus*. *J. Eukaryot. Microbiol.* 57, 40–47. <https://doi.org/10.1111/j.1550-7408.2009.00445.x>
- Corsaro D., Köhler M., Wylezich C., Venditti D., Walochnik J. and Michel R. 2018. New insights from molecular phylogenetics of amoebophagous fungi (Zoopagomycota, Zoopagales). *Parasitol. Res.* 117, 157–167. <https://doi.org/10.1007/s00436-017-5685-6>
- Cowie P.R. and Hannah F. 2006. Responses of four isolates of marine naked amoebae to reductions in salinity. *J. Exp. Mar. Biol. Ecol.* 337, 196–204. <https://doi.org/10.1016/j.jembe.2006.06.031>
- De Faria G., Da Cunha A.M. and Pinto C. 1922. Studien ueber Meeresprotozoen. *Estudos sobre Pro-tozoarios do mar. Mem.Inst. Oswaldo Cruz.* 15, 101–115. <https://doi.org/10.1590/S0074-02761922000200013>
- Dujardin F. 1841. *Histoire naturelle des zoo-*

phytes: Infusoires, comprenant la physiologie et la classification de ces animaux, et la manière de les étudier à l'aide du microscope. Roret, Paris. <https://doi.org/10.5962/bhl.title.10127>

Dunkerly J.S. 1921. *Rhabdamoeba marina* gen. n. et sp. n. Proc. R. Phys. Soc. Edinb. 20, 220–221.

Dyková I., Figueras A. and Peric Z. 2000. *Neoparamoeba* Page, 1987: Light and electron microscopic observations on six strains of different origin. Dis. Aquat. Org. 43, 217–223. <https://doi.org/10.3354/dao043217>

Dyková I., Fiala I., Lom J. and Lukeš J. 2003. *Perkinsiella amoebae*-like endosymbionts of *Neoparamoeba* spp., relatives of the kinetoplastid *Ichthyobodo*. Eur. J. Protistol. 39, 37–52. <https://doi.org/10.1078/0932-4739-00901>

Dyková I., Boháčová L., Fiala I., Macháčková B., Pecková H. and Dvořáková H. 2005a. Amoebae of the genera *Vannella* Bovee, 1965 and *Platyamoeba* isolated from fish and their phylogeny inferred from SSU rRNA gene and ITS sequences. Eur. J. Protistol. 41, 219–230. <https://doi.org/10.1016/j.ejop.2005.05.004>

Dyková I., Nowak B., Crosbie P., Fiala I., Pecková H., Adams M. and Dvořáková H. 2005b. *Neoparamoeba branchiphila* n. sp., and related species of the genus *Neoparamoeba* Page, 1987: Morphological and molecular characterization of selected strains. J. Fish Dis. 28, 49–64. <https://doi.org/10.1111/j.1365-2761.2004.00600.x>

Dyková I., Lom J., Dvořáková H., Pecková H. and Fiala I. 2007a. *Didymium*-like myxogastriids (class Mycetozoa) as endocommensals of sea urchins (*Sphaerechinus granularis*). Folia Parasitol. 54, 1–12. <https://doi.org/10.14411/fp.2007.001>

Dyková I., Nowak B., Pecková H., Fiala I., Crosbie P. and Dvořáková H. 2007b. Phylogeny of *Neoparamoeba* strains isolated from marine fish and invertebrates as inferred from SSU rDNA sequences. Dis. Aquat. Org. 74, 57–65. <https://doi.org/10.3354/dao074057>

Dyková I., Fiala I., Pecková H. and Dvořáková H. 2008a. Phylogeny of Flabellulidae (Amoebozoa: Leptomyxida) inferred from SSU rDNA sequences of the type strain of *Flabellula citata* Schaeffer, 1926 and newly isolated strains of marine amoebae. Folia Parasitol. 55, 256–264. <https://doi.org/10.14411/fp.2008.033>

Dyková I., Fiala I. and Pecková H. 2008b. *Neoparamoeba* spp. and their eukaryotic endosymbionts similar to *Perkinsiella amoebae* (Hollande, 1980): coevolution demonstrated by SSU rRNA gene phylogenies. Eur. J. Protistol. 44, 269–277.

<https://doi.org/10.1016/j.ejop.2008.01.004>

Dyková I., Pecková H. and Kostka M. 2008c. Introduction of *Mayorella gemmifera* Schaeffer, 1926 into phylogenetic studies of Amoebozoa. Acta Protozool. 47, 205–210.

Dyková I., Kostka M. and Pecková H. 2011. Three new species of the amoebozoan genus *Vexillifera* Schaeffer, 1926. Acta Protozool. 50, 55–63.

Dyková I. and Kostka M. 2013. Illustrated guide to culture collection of free-living amoebae. Academia, Praha.

English C.J. and Lima P.C. 2020. Defining the aetiology of amoebic diseases of aquatic animals: trends, hurdles and best practices. Dis. Aquat. Org. 142, 125–143. <https://doi.org/10.3354/dao03537>

English C.J., Tynl T., Botwright N.A., Barnes A.C., Wynne J.W., Lima P.C. et al. 2019. A diversity of amoebae colonise the gills of farmed Atlantic salmon (*Salmo salar*) with amoebic gill disease (AGD). Eur. J. Protistol. 67, 27–45. <https://doi.org/10.1016/j.ejop.2018.10.003>

Fahrni J.F., Bolivar I., Berney C., Nasonova E., Smirnov A. and Pawlowski J. 2003. Phylogeny of lobose amoebae based on actin and small-subunit ribosomal RNA genes. Mol. Biol. Evol. 20, 1881–1886. <https://doi.org/10.1093/molbev/msg201>

Feehan C.J., Johnson-Mackinnon J., Scheibling R.E., Lauzon-Guay J.S. and Simpson A.G. 2013. Validating the identity of *Paramoeba invadens*, the causative agent of recurrent mass mortality of sea urchins in Nova Scotia, Canada. Dis. Aquat. Org. 103, 209–227. <https://doi.org/10.3354/dao02577>

Fenchel T. 2010. The life history of *Flabellula baltica* Smirnov (Gymnamoebae, Rhizopoda): adaptations to a spatially and temporally heterogeneous environment. Protist. 161, 279–287. <https://doi.org/10.1016/j.protis.2009.10.005>

Fishbeck D. W. and Bovee E. C. 1993. Two new amoebae, *Striamoeba sparolata* n. sp. and *Flamella tiara* n. sp., from fresh water. Ohio J. Sci. 93, 134–139.

Folmer O., Black M., Hoeh W., Lutz R. and Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Mol. Mar. Biol. Biotechnol. 3, 294–299.

Frenzel J. 1897. Untersuchungen über die mikroskopische Fauna Argentinien. I, II. Die Rhizopoden und Helioamöben. Verlag von Erwin Nägele, Stuttgart.

Garcia A., Goni P., Clavel A., Lobez S., Fernandez M.T. and Ormad M.P. 2011. Potentially pathogenic free-living amoebae (FLA) isolated

- in Spanish wastewater treatment plants. Environ. Microbiol. Rep. 3, 622–626. <https://doi.org/10.1111/j.1758-2229.2011.00271.x>
- Garstecki T. and Arndt H. 2000. Seasonal abundances and community structure of benthic rhizopods in shallow lagoons of the southern Baltic Sea. Eur. J. Protistol. 36, 103–115. [https://doi.org/10.1016/S0932-4739\(00\)80027-9](https://doi.org/10.1016/S0932-4739(00)80027-9)
- Gast R.J., Fuerst P.A. and Byers T.J. 1994. Discovery of group I introns in the nuclear small subunit ribosomal RNA genes of *Acanthamoeba*. Nucleic Acids Res. 22, 592–596. <https://doi.org/10.1093/nar/22.4.592>
- Gast R.J., Ledee D.R., Fuerst P.A. and Byers T.J. 1996. Subgenus systematics of *Acanthamoeba*: four nuclear 18S rDNA sequence types. J. Eukaryot. Microbiol. 43, 498–504. <https://doi.org/10.1111/j.1550-7408.1996.tb04510.x>
- Geisen S., Kudryavtsev A., Bonkowski M. and Smirnov A. 2014. Discrepancy between species borders at morphological and molecular levels in the genus *Cochliopodium* (Amoebozoa, Himatismenida), with the description of *Cochliopodium plurinucleolum* n. sp. Protist. 165, 364–383. <https://doi.org/10.1016/j.protis.2014.04.002>
- Gile G.H., Faktorová D., Castlejohn C.A., Burger G., Lang B.F., Farmer M.A. et al. 2009. Distribution and phylogeny of EFL and EF-1 α in Euglenozoa suggest ancestral co-occurrence followed by differential loss. PLoS One. 4, e5162. <https://doi.org/10.1371/journal.pone.0005162>
- Glotova A. and Smirnov A. 2017. Description of *Flamella daurica* n. sp., with notes on the phylogeny of the genus *Flamella* and related taxa. Eur. J. Protistol. 58, 164–174. <https://doi.org/10.1016/j.ejop.2017.02.003>
- Glücksman E., Snell E.A., Berney C., Chao E.E., Bass D. and Cavalier-Smith T. 2011. The novel marine gliding zooflagellate genus *Mantamonas* (Mantamonadida ord. n.: Apusozoa). Protist. 162, 207–221. <https://doi.org/10.1016/j.protis.2010.06.004>
- Gonzalez-Robles A., Salazar-Villatoro L., Omana-Molina M., Reyes-Batlle M., Martín-Navarro C.M. and Lorenzo-Morales J. 2014. Morphological features and in vitro cytopathic effect of *Acanthamoeba griffini* trophozoites isolated from a clinical case. J. Parasitol. Res. 256310. <https://doi.org/10.1155/2014/256310>
- Goodfellow L.P., Belcher J. H. and Page F.C. 1974. A light- and electron-microscopical study of *Sappinia diploidea*, a sexual amoeba. Protistologica. 2, 207–216.
- Goodkov A.V. 1988. *Korotnevella* nom. nov. — new generic name for scale-bearing *Mayorella*-like amoebae. Zoologicheskyy Zhurnal. 67, 1728–1730. (in Russian with English summary).
- Goodkov A.V. and Buryakov V.Y. 1987. A new species of the limax amoeba (Sarcodina, Lobosea) from the White Sea. Zoologicheskyy Zhurnal. 66, 928–930 (in Russian with English summary)
- Goodkov A.V. and Buryakov V.Y. 1988. *Mayorella dactylifera* sp. n. (Gymnamoebia, Paramoebidae) and brief review of marine species of mayorelles. Zoologicheskyy Zhurnal. 67, 927–931 (in Russian with English summary).
- Grassi B. 1881. Intorno ai chetognati. Reale Istituto Lombardo di Scienze e Lettere, Series. 2 (14), 185–224.
- Grell K.G. 1961. Über den Nebenkörper von *Paramoeba eilhardi* Schaudinn. Arch. Protistenkd. 105, 303–312.
- Grell K.G. 1966. Amöben der Familie Stereomyxidae. Arch. Protistenkd. 109, 147–154.
- Grell K.G. 1988. *Corallomyxa multipara* n. sp., ein plasmodialer Rhizopode von der ostaustralischen Küste. Arch. Protistenkd. 136, 117–138. [https://doi.org/10.1016/S0003-9365\(88\)80001-0](https://doi.org/10.1016/S0003-9365(88)80001-0)
- Grell K.G. 1991. *Corallomyxa nipponica* n. sp. and the phylogeny of plasmodial protists. Arch. Protistenkd. 140, 303–320. [https://doi.org/10.1016/S0003-9365\(11\)80195-8](https://doi.org/10.1016/S0003-9365(11)80195-8)
- Grell K.G. and Benwitz G. 1966. Notizen: Die Zellhülle von *Paramoeba eilhardi* Schaudinn. Z. Naturforsch. B 21, 600–601. <https://doi.org/10.1515/znb-1966-0631>
- Grell K.G. and Benwitz G. 1970. Ultrastruktur mariner Amöben. I. *Paramoeba eilhardi* Schaudinn. Arch. Protistenkd. 112, 119–137.
- Grell K.G. and Benwitz G. 1978. Ultrastruktur mariner Amöben. IV. *Corallomyxa chattoni* n. sp. Arch. Protistenkd. 120, 287–300. [https://doi.org/10.1016/S0003-9365\(78\)80004-9](https://doi.org/10.1016/S0003-9365(78)80004-9)
- Gruber A. 1882a. Beiträge zur Kenntnis der Amöben. Z. Wiss. Zool. 36, 459–470.
- Gruber A. 1882b. Contributions to the knowledge of the amoebae. Ann. Mag. Nat. Hist. Ser. 5. 9, 106–116.
- Gruber A. 1883a. Untersuchungen über einige Protozoen. Z. Wiss. Zool. 38, 45–70.
- Gruber A. 1883b. Investigations upon some Protozoa. Ann. Mag. Nat. Hist. Ser. 5. 11, 266–276. <https://doi.org/10.1080/00222938309459143>
- Gruber A. 1885. Studien über Amöben. Z. Wiss. Zool. 41, 186–225.

Gruber A. 1887–1888. Enumerazione dei protozoi raccolti nel porto di Genova. *Annali Museo Civico Storia Naturale Genova* 25, 535–553.

Hansen H., Botwright N.A., Cook M.T., Douglas A., Downes J., Gallagher M.D. et al. 2019. Genetic diversity among geographically distant isolates of *Neoparamoeba perurans*. *Dis. Aquat. Org.* 137, 81–87. <https://doi.org/10.3354/dao03433>

Hauer G. and Rogerson A. 2005a. Remarkable salinity tolerance of seven species of naked amoebae (gymnamoebae). *Hydrobiologia*. 549, 33–42. <https://doi.org/10.1007/s10750-005-2210-1>

Hauer G. and Rogerson A. 2005b. Heterotrophic protozoa from hypersaline environments. In: *Adaptation to life at high salt concentrations in archaea, bacteria, and eukarya*. Springer, Dordrecht, pp. 519–539. https://doi.org/10.1007/1-4020-3633-7_33

Hauer G., Rogerson A. and Anderson O.R. 2001. *Platyamoeba pseudovannellida* n. sp., a naked amoeba with wide salt tolerance isolated from the Salton Sea, California. *J. Eukaryot. Microbiol.* 48, 663–669. <https://doi.org/10.1111/j.1550-7408.2001.tb00206.x>

Hebert P.D., Cywinska A., Ball S.L. and DeWaard J.R. 2003. Biological identifications through DNA barcodes. *Proc. R. Soc. London. B: Biol. Sci.* 270, 313–321. <https://doi.org/10.1098/rspb.2002.2218>

Heredero-Bermejo I., Criado-Fornelio A., De Fuentes I., Soliveri J., Copa-Patino J.L. and Perez-Serrano J. 2015. Characterization of a human-pathogenic *Acanthamoeba griffini* isolated from a contact lens-wearing keratitis patient in Spain. *Parasitology*. 142, 363–373. <https://doi.org/10.1017/S0031182014001140>

Hogue M.J. 1914. Studies in the life history of an amoeba of the limax group. *Vahlkampfia calkensi*. *Arch. Protistenkd.* 35, 154–163.

Hollande A. 1980. Identification du parasome (Nebenkern) de *Janickina pigmentifera* a un symbionte (*Perkinsiella amoebae* nov gen - nov sp.) apparenté aux flagellés kinetoplastidies. *Protistologica* 16, 613–625.

Hollande A., Nicolas G. and Escaig J. 1981. Vêtue glycostylique et ultrastructure d'une Amibe marine libre (*Mayorella pussardi* nov. sp.: Paramoebidae) observée après congélation ultrarapide suivie de cryosubstitution. *Protistologica*. 11, 147–154.

Hopkins D.L. 1938. Adjustment of the marine amoeba, *Flabellula mira* Schaeffer, to changes in the total salt concentration of the outside medium. *Biol. Bull.* 75, 337.

Jahn T.L. and Bovee E.C. 1965. Mechanisms of movement in taxonomy of Sarcodina. I. As a basis for a new major dichotomy into two classes, Autotractea and Hydraulea. *Am. Midl. Nat.* 73, 30–40. <https://doi.org/10.2307/2423319>

Jahn T.L., Bovee E.C. and Griffith D.L. 1974. Taxonomy and evolution of the Sarcodina: a reclassification. *Taxon* 23, 483–496. <https://doi.org/10.2307/1218771>

Janicki C. 1912. Paramoebenstudien. (*P. pigmentifera* Grassi und *P. chaetognathi* Grassi). *Z. Wiss. Zool.* 103, 449–518.

Jones D.T. 1945. Two protozoans from Great Salt Lake, *Amoeba flowersi* sp. n. and *Euglena chamberlini* sp. n. *Bull. Univ. Utah biol. Ser.* 8, 3–10.

Jones G. 1985. *Paramoeba invadens* n. sp. (Amoebida, Paramoebidae), a pathogenic amoeba from the Sea Urchin, *Strongylocentrotus droebachiensis*, in Eastern Canada. *J. Protozool.* 32, 564–569. <https://doi.org/10.1111/j.1550-7408.1985.tb03075.x>

Jones G.M. and Scheibling R.E. 1985. *Paramoeba* sp. (Amoebida, Paramoebidae) as the possible causative agent of sea urchin mass mortality in Nova Scotia. *J. Parasitol.* 71, 559–565. <https://doi.org/10.2307/3281424>

Kang S., Tice A.K., Spiegel F.W., Silberman J.D., Pánek T., Čepička I. et al. 2017. Between a pod and a hard test: the deep evolution of amoebae. *Mol. Biol. Evol.* 34, 2258–2270. <https://doi.org/10.1093/molbev/msx162>

Karlsbakk E., Olsen A.B., Einen A.-C.B., Mo T.A., Fiksdal I.U., Aase H. et al. 2013. Amoebic gill disease due to *Paramoeba perurans* in ballan wrasse (*Labrus bergylta*). *Aquaculture*. 412, 41–44. <https://doi.org/10.1016/j.aquaculture.2013.07.007>

Keeling P.J., Burki F., Wilcox H.M., Allam B., Allen E.E., Amaral Zettler L.A. et al. 2014. The marine microbial eukaryote transcriptome sequencing project (MMETSP): illuminating the functional diversity of eukaryotic life in the oceans through transcriptome sequencing. *PLoS Biology* 12, e1001889. <https://doi.org/10.1371/journal.pbio.1001889>

Kent W.S. 1880. A manual of the Infusoria: including a description of all known flagellate, ciliate, and tentaculiferous protozoa, British and foreign, and an account of the organization and the affinities of the sponges, 1. David Bogue, London. <https://doi.org/10.5962/bhl.title.20943>

Khan N.A., Jarroll E.L. and Paget T.A. 2002. Molecular and physiological differentiation between pathogenic and nonpathogenic *Acanthamoeba*. *Curr.*

Microbiol. 45, 197–202. <https://doi.org/10.1007/s00284-001-0108-3>

Khlebovich V.V. 1968. Some peculiar features of the hydrochemical regime and the fauna of mesohaline waters. *Mar. Biol.* 2, 47–49. <https://doi.org/10.1007/BF00351637>

Khlebovich V.V. and Abramova E.N. 2000. Some problems of crustacean taxonomy related to the phenomenon of horohalinicum. *Hydrobiologia.* 417, 109–113. <https://doi.org/10.1023/A:1003863623267>

Kim W.S., Kong K.H., Kim J.O. and Oh M.J. 2016. Amoebic gill infection in coho salmon *Oncorhynchus kisutch* farmed in Korea. *Dis. Aquat. Org.* 121, 75–78. <https://doi.org/10.3354/dao03037>

Klimov V.I. and Zlatogursky V.V. 2016. Light- and electron-microscopical study of *Belonocystis marina* sp. nov. (Eukaryota: incertae sedis). *Protist.* 167, 479–489. <https://doi.org/10.1016/j.protis.2016.07.003>

Koltas I.S., Eroglu F., Erdem E., Yagmur M. and Tanır F. 2015. The role of domestic tap water on *Acanthamoeba* keratitis in non-contact lens wearers and validation of laboratory methods. *Parasitol. Res.* 114, 3283–3289. <https://doi.org/10.1007/s00436-015-4549-1>

Korotneff A. 1879. Etudes sur les Rhizopodes. *Arch. Zool. Exp.* 8, 467–482.

Kostka M., Lares-Jiménez L.F., Tylm T. and Dyková I. 2017. *Copromyxa laresi* n. sp. (Amoebozoa: Tubulinea) and transfer of *Cashia limacoides* (Page, 1967) to *Copromyxa* Zopf, 1885. *J. Euk. aryt. Microbiol.* 64, 173–182. <https://doi.org/10.1111/jeu.12349>

Kudryavtsev A.A. 1999. The first isolation of *Cochliopodium gulosum* Schaeffer, 1926 (Lobosea, Himatistenida) since its initial description. I. Light-microscopical investigation. *Protistology.* 1, 72–75.

Kudryavtsev A.A. 2000. The first isolation of *Cochliopodium gulosum* Schaeffer, 1926 (Lobosea, Himatistenida) since its initial description. II. Electron-microscopical study and redescription. *Protistology.* 1, 110–112.

Kudryavtsev A.A. 2004. Description of *Cochliopodium spiniferum* sp. n., with notes on the species identification within the genus *Cochliopodium*. *Acta Protozool.* 43, 345–349.

Kudryavtsev A. 2006. “Minute” species of *Cochliopodium* (Himatistenida): Description of three new fresh- and brackish-water species with a new diagnosis for *Cochliopodium minus* Page, 1976. *Eur. J. Protistol.* 42, 77–89. <https://doi.org/10.1016/j.ejop.2005.12.002>

Kudryavtsev A. 2012. Microscopic evidence for inclusion of *Parvamoeba* Rogerson, 1993 into the order Himatistenida (Amoebozoa). *Eur. J. Protistol.* 48, 85–88. <https://doi.org/10.1016/j.ejop.2011.07.003>

Kudryavtsev A., Bernhard D., Schlegel M., Chao E. E.-Y. and Cavalier-Smith T. 2005. 18S ribosomal RNA gene sequences of *Cochliopodium* (Himatistenida) and the phylogeny of Amoebozoa. *Protist.* 156, 215–224. <https://doi.org/10.1016/j.protis.2005.03.003>

Kudryavtsev A. and Smirnov A. 2006. *Cochliopodium gallicum* n. sp. (Himatistenida), an amoeba bearing unique scales, from cyanobacterial mats in the Camargue (France). *Eur. J. Protistol.* 42, 3–7. <https://doi.org/10.1016/j.ejop.2005.08.001>

Kudryavtsev A., Wylezich C., Schlegel M., Walochnik J. and Michel R. 2009. Ultrastructure, SSU rRNA gene sequences and phylogenetic relationships of *Flamella* Schaeffer, 1926 (Amoebozoa), with description of three new species. *Protist.* 160, 21–40. <https://doi.org/10.1016/j.protis.2008.09.004>

Kudryavtsev A., Pawlowski J. and Hausmann K. 2011a. Description of *Paramoeba atlantica* n. sp. (Amoebozoa, Dactylopodida) – a marine amoeba from the Eastern Atlantic, with emendation of the dactylopodid families. *Acta Protozool.* 50, 239–253.

Kudryavtsev A., Wylezich C. and Pawlowski J. 2011b. *Ovalopodium desertum* n. sp. and the phylogenetic relationships of Cochliopodiidae (Amoebozoa). *Protist.* 162, 571–589. <https://doi.org/10.1016/j.protis.2011.04.002>

Kudryavtsev A. and Pawlowski J. 2013. *Squamamoeba japonica* n. g. n. sp. (Amoebozoa): a deep-sea amoeba from the Sea of Japan with a novel cell coat structure. *Protist.* 164, 13–23. <https://doi.org/10.1016/j.protis.2012.07.003>

Kudryavtsev A., Brown M. W., Tice A., Spiegel F.W., Pawlowski J. and Anderson O.R. 2014. A revision of the order Pellitida Smirnov et al., 2011 (Amoebozoa, Discosea) based on ultrastructural and molecular evidence, with description of *Endostelium crystalliferum* n. sp. *Protist.* 165, 208–229. <https://doi.org/10.1016/j.protis.2014.02.003>

Kudryavtsev A. and Pawlowski J. 2015. *Cunea* n. g. (Amoebozoa, Dactylopodida) with two cryptic species isolated from different areas of the ocean. *Eur. J. Protistol.* 51, 197–209. <https://doi.org/10.1016/j.ejop.2015.04.002>

Kudryavtsev A. and Gladkikh A. 2017. Two new species of *Ripella* (Amoebozoa, Vannellida) and unusual intragenomic variability in the SSU rRNA gene of this genus. *Eur. J. Protistol.* 61, 92–106.

<https://doi.org/10.1016/j.ejop.2017.09.003>

Kudryavtsev A., Pawlowski J. and Smirnov A. 2018. More amoebae from the deep-sea: two new marine species of *Vexillifera* (Amoebozoa, Dactylopodida) with notes on taxonomy of the genus. *Eur. J. Protistol.* 66, 9–25. <https://doi.org/10.1016/j.ejop.2018.07.001>

Kudryavtsev A. and Volkova E. 2018. *Clydonella sawyeri* n. sp. (Amoebozoa, Vannellida): morphological and molecular study and a re-definition of the genus *Clydonella* Sawyer, 1975. *Eur. J. Protistol.* 63, 62–71. <https://doi.org/10.1016/j.ejop.2018.01.008>

Kudryavtsev A., Volkova E. and Plotnikov A. 2019. *Vannella samoroda* n. sp. (Amoebozoa) – first member of the genus from a continental saline habitat placed in a molecular tree. *Eur. J. Protistol.* 71, 125634. <https://doi.org/10.1016/j.ejop.2019.125634>

Kudryavtsev A. and Volkova E. 2020. *Cunea russae* n. sp. (Amoebozoa, Dactylopodida), another cryptic species of *Cunea* Kudryavtsev and Pawlowski, 2015, inhabits a continental brackish-water biotope. *Eur. J. Protistol.* 73, 125685. <https://doi.org/10.1016/j.ejop.2020.125685>

Kudryavtsev A.A., Volkova E.N. and Voytinsky F.P. 2020. Morphological and molecular investigation of *Vexillifera* cf. *armata* Page, 1979 (Amoebozoa: Dactylopodida) isolated from the Pacific Ocean. *Invert. Zool.* 17, 385–402. <https://doi.org/10.15298/invertzool.17.4.04>

Kudryavtsev A., Völcker E., Clauß S. and Pawlowski J. 2021. *Ovalopodium rosalinum* sp. nov., *Planopodium haveli* gen. nov, sp. nov., *Planopodium desertum* comb. nov. and new insights into phylogeny of the deeply branching members of the order Himatismenida (Amoebozoa). *Int. J. Sys. Evol. Microbiol.* 71, 004737. <https://doi.org/10.1099/ijsem.0.004737>

Kufferath H. 1952. Recherches sur le plancton de la Mer Flamande (Mer de Nord Méridionale). *Bull. Inst. R. Sci. nat. Belg.* 28, 1–39.

Kühn S.F. 1996/97. *Rhizamoeba schneppii* sp. nov., a naked amoeba feeding on marine diatoms (North Sea, German Bight). *Arch. Protistenkd.* 147, 277–282. [https://doi.org/10.1016/S0003-9365\(97\)80054-1](https://doi.org/10.1016/S0003-9365(97)80054-1)

Kuiper M.W., Valster R.M., Wullings B.A., Boonstra H., Smidt H. and van der Kooij D. 2006. Quantitative detection of the free-living amoeba *Hartmannella vermiformis* in surface water by using real-time PCR. *App. Env. Microbiol.* 72, 5750–5756. <https://doi.org/10.1128/AEM.00085-06>

Lahr D. J., Grant J., Nguyen T., Lin J. H. and Katz L. A. 2011. Comprehensive phylogenetic reconstruction of Amoebozoa based on concatenated analyses of SSU-rDNA and actin genes. *PLoS One* 6, e22780. <https://doi.org/10.1371/journal.pone.0022780>

Lahr D. J., Grant J., Molestina R., Katz L. A. and Anderson O. R. 2015. *Sapocribum chincoteaguense* n. gen. n. sp.: a small, scale-bearing amoebozoan with flabellinid affinities. *J. Eukaryot. Microbiol.* 62, 444–453. <https://doi.org/10.1111/jeu.12199>

Larsen J. and Patterson D.J. 1990. Some flagellates (Protista) from tropical marine sediments. *J. Nat. Hist.* 24, 801–937. <https://doi.org/10.1080/00222939000770571>

Ledee D.R., Hay J., Byers T.J., Seal D.V. and Kirkness C.M. 1996. *Acanthamoeba griffini*. Molecular characterization of a new corneal pathogen. *Invest. Ophthalmol. Vis. Sci.* 37, 544–550.

Ledee D.R., Booton G.C., Awwad M.H., Sharma S., Aggarwal R.K., Niszl I.A. et al. 2003. Advantages of using mitochondrial 16S rDNA sequences to classify clinical isolates of *Acanthamoeba*. *Invest. Ophthalmol. Vis. Sci.* 44, 1142–1149. <https://doi.org/10.1167/iovs.02-0485>

Leidy J. 1879. Freshwater rhizopods of North America. U.S. Geol. Survey of the Territories, Washington. <https://doi.org/10.5962/bhl.title.4759>

Lemmermann E. 1914. Pantostomatinae, Promastiginae and Distomatinae. *Die Süßwasserflora Deutschlands, Österreichs und der Schweiz.* 1, 1–137.

Levine N.D., Corliss J.O., Cox F.E.G., Deroux G., Grain J., Honigberg B.M. et al. 1980. A newly revised classification of the Protozoa. *J. Protozool.* 27, 37–58. <https://doi.org/10.1111/j.1550-7408.1980.tb04228.x>

Lima P.C., Botwright N.A., Harris J.O. and Cook M. 2014. Development of an in vitro model system for studying bacterially expressed dsRNA-mediated knockdown in *Neoparamoeba* genus. *Mar. Biotechnol.* 16, 447–455. <https://doi.org/10.1007/s10126-014-9561-4>

Lin S. and Zhang H. 2005. Isolation of mitochondrial cytochrome b gene and development of a real-time quantitative PCR assay for detecting *Neoparamoeba aestuarina*. *J. Shellfish Res.* 24, 733–739. [https://doi.org/10.2983/0730-8000\(2005\)24\[733:IOMCBG\]2.0.CO;2](https://doi.org/10.2983/0730-8000(2005)24[733:IOMCBG]2.0.CO;2)

Lotonin K. and Smirnov A. 2020. *Stygamoeba cauta* n. sp. (Amoebozoa, Discosea) – a new brackish-water species from Nivå Bay (Baltic Sea, The Sound). *Eur. J. Protistol.* 72, 125660. <https://doi.org/10.1016/j.ejop.2020.125660>

[org/10.1016/j.ejop.2019.125660](https://doi.org/10.1016/j.ejop.2019.125660)

Martín-Pérez T., Criado-Fornelio A., Martínez J., Blanco M.A., Fuentes I. and Pérez-Serrano J. 2017. Isolation and molecular characterization of *Acanthamoeba* from patients with keratitis in Spain. *Eur. J. Protistol.* 61, 244–252. <https://doi.org/10.1016/j.ejop.2017.06.009>

Mast S. O. 1926. Structure, movement, locomotion, and stimulation in amoeba. *J. Morphol.* 41, 347–425. <https://doi.org/10.1002/jmor.1050410205>

Mereschkowsky von C. 1879. Studien über Protozoen des nordlichen Russland. *Arch. Mikr. Anat.* 16, 153–248. <https://doi.org/10.1007/BF02956383>

Mesentsev Y.S. and Smirnov A.V. 2019. *Thecamoeba cosmophorea* n. sp. (Amoebozoa, Discosea, Thecamoebida) – an example of sibling species within the genus *Thecamoeba*. *Eur. J. Protistol.* 67, 132–141. <https://doi.org/10.1016/j.ejop.2018.12.003>

Mesentsev Y.S., Kamyshatskaya O.G. and Smirnov A.V. 2020. *Thecamoeba foliovenanda* n. sp. (Amoebozoa, Discosea, Thecamoebida) – one more case of sibling species among amoebae of the genus *Thecamoeba*. *Eur. J. Protistol.* 76, 125716. <https://doi.org/10.1016/j.ejop.2020.125716>

Mesentsev Y. and Smirnov A. 2021. *Thecamoeba astrologa* n. sp. – a new species of the genus *Thecamoeba* (Amoebozoa, Discosea, Thecamoebida) with an unusually polymorphic nuclear structure. *Eur. J. Protistol.* 81, 125837. <https://doi.org/10.1016/j.ejop.2021.125837>

Michel R. and Smirnov A.V. 1999. The genus *Flamella* Schaeffer, 1926 (Lobosea, Gymnamoebia), with description of two new species. *Eur. J. Protistol.* 35, 403–410. [https://doi.org/10.1016/S0932-4739\(99\)80049-2](https://doi.org/10.1016/S0932-4739(99)80049-2)

Mikrjukov K.A. and Mylnikov A.P. 1998. The fine structure of a carnivorous multiflagellar protist *Multicilia marina* Cienkowski, 1881 (flagellata incertae sedis). *Eur. J. Protistol.* 34, 391–401. [https://doi.org/10.1016/S0932-4739\(98\)80008-4](https://doi.org/10.1016/S0932-4739(98)80008-4)

Milanez G., Masangkay F., Hapan F., Bencito T., Lopez M., Soriano J. et al. 2020. Detection of *Acanthamoeba* spp. in two major water reservoirs in the Philippines. *J. Water Health* 18, 118–126. <https://doi.org/10.2166/wh.2020.190>

Möbius K. 1888. Bruchstücke einer Rhizopodenfauna der Kieler Bucht. *Abh. Preuss. Akad. Wiss., Berlin*, pp. 1–31.

Moran D.M., Anderson O.R., Dennett M.R., Caron D.A. and Gast R.J. 2007. A description of seven antarctic marine gymnamoebae including a new subspecies, two new species and a new genus: *Neoparamoeba aestuarina antarctica* n. subsp., *Platyamoeba oblongata* n. sp., *Platyamoeba contorta* n. sp. and *Vermistella antarctica* n. gen. n. sp. *J. Eukaryot. Microbiol.* 54, 169–183. <https://doi.org/10.1111/j.1550-7408.2007.00249.x>

tyamoeba oblongata n. sp., *Platyamoeba contorta* n. sp. and *Vermistella antarctica* n. gen. n. sp. *J. Eukaryot. Microbiol.* 54, 169–183. <https://doi.org/10.1111/j.1550-7408.2007.00249.x>

Mullen T.E., Nevis K.R., O’Kelly C.J., Gast R.J. and Frasca J.S. 2005. Nuclear small-subunit ribosomal RNA gene-based characterization, molecular phylogeny and PCR detection of the *Neoparamoeba* from western long island sound lobster. *J. Shellfish Res.* 24, 719–731. [https://doi.org/10.2983/0730-8000\(2005\)24\[719:NSRRGC\]2.0.CO;2](https://doi.org/10.2983/0730-8000(2005)24[719:NSRRGC]2.0.CO;2)

Nassonova E., Smirnov A., Fahrni J. and Pawlowski J. 2010. Barcoding amoebae: comparison of SSU, ITS and COI genes as tools for molecular identification of naked lobose amoebae. *Protist.* 161, 102–115. <https://doi.org/10.1016/j.protis.2009.07.003>

Nikolaev S.I., Berney C., Petrov N.B., Mylnikov A.P., Fahrni J.F. and Pawlowski J. 2006. Phylogenetic position of *Multicilia marina* and the evolution of Amoebozoa. *Int. J. Syst. Evol. Microbiol.* 56, 1449–1458. <https://doi.org/10.1099/ijs.0.63763-0>

Nowak B.F., Bryan J. and Jones S.R.M. 2010. Do salmon lice, *Lepeophtheirus salmonis*, have a role in the epidemiology of amoebic gill disease caused by *Neoparamoeba perurans*? *J. Fish Dis.* 33, 683–687. <https://doi.org/10.1111/j.1365-2761.2010.01158.x>

Nowak B.F. and Archibald J.M. 2018. Opportunistic but lethal: the mystery of paramoebae. *Trends Parasitol.* 34, 404–419. <https://doi.org/10.1016/j.pt.2018.01.004>

Nylund A., Watanabe K., Nylund S., Karlsen M., Saether P.A., Arnesen C.E. et al. 2008. Morphogenesis of salmonid gill poxvirus associated with proliferative gill disease in farmed Atlantic salmon (*Salmo salar*) in Norway. *Arch. Virol.* 153, 1299–1309. <https://doi.org/10.1007/s00705-008-0117-7>

O’Kelly C.J., Peglar M.T., Black M.N., Sawyer T.K. and Nerad T.A. 2001. *Korotnevella hemistylepis* N. Sp. and *Korotnevella monacantholepis* N. Sp. (Paramoebidae), two new scale-covered mesohaline amoebae. *J. Eukaryot. Microbiol.* 48, 655–662. <https://doi.org/10.1111/j.1550-7408.2001.tb00205.x>

Page F.C. 1968. Generic criteria for *Flabellula*, *Rugipes* and *Hyalodiscus*, with descriptions of species. *Eur. J. Protistol.* 15, 9–26. <https://doi.org/10.1111/j.1550-7408.1968.tb02084.x>

Page F.C. 1970a. Two new species of *Paramoeba* from Maine. *J. Protozool.* 17, 421–427. <https://doi.org/10.1111/j.1550-7408.1970.tb04706.x>

Page F.C. 1970b. *Mastigamoeba aspera* from estuarine tidal pools in Maine. Trans. Amer. Microsc. Soc. 89, 197–200. <https://doi.org/10.2307/3224374>

Page F.C. 1971a. Two marine species of *Flabellula* (Amoebida, Mayorellidae). J. Protozool. 18, 37–44. <https://doi.org/10.1111/j.1550-7408.1971.tb03277.x>

Page F.C. 1971b. A comparative study of five fresh-water and marine species of Thecamoebidae. Trans. Amer. Microsc. Soc. 90, 157–173. <https://doi.org/10.2307/3225022>

Page F.C. 1972a. *Rhizamoeba polyura* n. g., n. sp., and uroidal structures as a taxonomic criterion for amoebae. Trans. Amer. Microsc. Soc. 91, 502–513. <https://doi.org/10.2307/3225479>

Page F.C. 1972b. A study of two *Mayorella* species and proposed union of the families Mayorellidae and Paramoebidae (Rhizopodea, Amoebida). Arch. Protistenkd. 114, 404–420.

Page F.C. 1973. *Paramoeba*: a common marine genus. Hydrobiologia 41, 183–188. <https://doi.org/10.1007/BF00016444>

Page F.C. 1974a. Some marine *Platyamoeba* of East Anglia. J. Mar. Biol. Assoc. U. K. 54, 651–664. <https://doi.org/10.1017/S0025315400022827>

Page F.C. 1974b. A further study of taxonomic criteria for limax amoebae, with descriptions of new species and a key to genera. Arch. Protistenkd. 116, 149–184.

Page F.C. 1976a. A revised classification of the Gymnamoebia (Protozoa: Sarcodina). Zool. J. Linn. Soc. 58, 61–77. <https://doi.org/10.1111/j.1096-3642.1976.tb00820.x>

Page F.C. 1976b. An illustrated key to freshwater and soil amoebae with notes on cultivation and ecology. Freshwater Biol. Assoc., Ambleside.

Page F.C. 1976c. Some comparative notes on the occurrence of Gymnamoebia (Protozoa: Sarcodina) in British and American habitats. Trans. Amer. Microsc. Soc. 95, 385–394. <https://doi.org/10.2307/3225131>

Page F.C. 1977. The genus *Thecamoeba* (Protozoa, Gymnamoebia) species distinctions, locomotive morphology, and protozoan prey. J. Nat. Hist. 11, 25–63. <https://doi.org/10.1080/00222937700770031>

Page F.C. 1978. An electron-microscopical study of *Thecamoeba proteoides* (Gymnamoebia), intermediate between Thecamoebidae and Amoebidae. Protistologica. 14, 77–85.

Page F.C. 1979a. *Vexillifera armata* n. sp. (Gymnamoebia, Paramoebidae), an estuarine amoeba

with distinctive surface structures and trichocyst-like bodies. Protistologica. 15, 111–122. [https://doi.org/10.1016/S0003-9365\(79\)80017-2](https://doi.org/10.1016/S0003-9365(79)80017-2)

Page F.C. 1979b. Two genera of marine amoebae (Gymnamoebia) with distinctive surface structures *Vannella* Bovee 1965, and *Pseudoparamoeba* n. gen., with two new species of *Vannella* Bovee. Protistologica. 15, 245–257.

Page F.C. 1979c. The fine structure of *Vexillifera bacillipedes* (Amoebida, Paramoebidae). Arch. Protistenkd. 122, 9–19. [https://doi.org/10.1016/S0003-9365\(79\)80017-2](https://doi.org/10.1016/S0003-9365(79)80017-2)

Page F.C. 1980a. A key to marine species of *Vannella* (Sarcodina: Gymnamoebia), with descriptions of new species. J. Mar. Biol. Ass. UK. 60, 929–946. <https://doi.org/10.1017/S0025315400041990>

Page F.C. 1980b. Fine structure of some marine strains of *Platyamoeba* (Gymnamoebia, Thecamoebidae). Protistologica. 16, 605–612.

Page F.C. 1980c. A light- and electron-microscopical comparison of limax and flabellate marine amoebae belonging to four genera. Protistologica. 16, 57–78.

Page F.C. 1981a. A light- and electron-microscopical study of *Protacanthamoeba caledonica* n. sp., type-species of *Protacanthamoeba* n. g. (Amoebida, Acanthamoebidae). J. Protozool. 28, 70–78. <https://doi.org/10.1111/j.1550-7408.1981.tb02807.x>

Page F.C. 1981b. *Mayorella* Schaeffer, 1926, and *Hollandella* n.g. (Gymnamoebia), distinguished by surface structure and other characters, with comparisons of three species. Protistologica. 17, 543–562.

Page F.C. 1983a. Marine gymnamoebae. Institute of Terrestrial Ecology, Cambridge.

Page F.C. 1983b. Three freshwater species of *Mayorella* (Amoebida) with a cuticle. Arch. Protistenkd. 127, 201–221. [https://doi.org/10.1016/S0003-9365\(83\)80037-2](https://doi.org/10.1016/S0003-9365(83)80037-2)

Page F.C. 1985. The limax amoebae: comparative fine structure of the Hartmannellidae (Lobosea) and further comparisons with the Vahlkampfiidae (Heterolobosea). Protistologica. 21, 361–383.

Page F.C. 1987. The classification of ‘naked’ amoebae (Phylum Rhizopoda). Arch. Protistenkd. 133, 199–217. [https://doi.org/10.1016/S0003-9365\(87\)80053-2](https://doi.org/10.1016/S0003-9365(87)80053-2)

Page F.C. 1988. A new key to freshwater and soil gymnamoebae. Freshwater Biological Association, Ambleside.

Page F.C. 1991. Nackte Rhizopoda und Helio-

zoa. Protozoenfauna 2. G. Fischer, Stuttgart, New York.

Page F.C. and Blakey S.M. 1979. Cell surface structure as a taxonomic character in the Thecamoebidae (Protozoa: Gymnamoebia). Zool. J. Linn. Soc. 66, 113–135. <https://doi.org/10.1111/j.1096-3642.1979.tb01905.x>

Page F.C. and Baldock B. M. 1980. *Polychaos fasciculatum* (Penard 1902) (Amoebida): a light- and electron-microscopical study. Arch. Protistenkd. 123, 221–235. [https://doi.org/10.1016/S0003-9365\(80\)80007-8](https://doi.org/10.1016/S0003-9365(80)80007-8)

Page F.C. and Willumsen N.B.S. 1980. Some observations on *Gocevia placopus* (Hülsmann, 1974), an amoeba with a flexible test, and on *Gocevia*-like organisms from Denmark, with comments on the genera *Gocevia* and *Hyalodiscus*. J. Nat. Hist. 14, 413–431. <https://doi.org/10.1080/00222938000770361>

Page F.C. and Willumsen N.B.S. 1983. A light- and electron-microscopical study of *Paraflabellula reniformis* (Schmoller, 1964), type species of a genus of amoebae (Amoebida, Flabellulidae) with sub-pseudopodia. Protistologica. 19, 567–575.

Page F.C. and Kalinina L.V. 1984. *Amoeba leningradensis* n. sp. (Amoebidae): a taxonomic study incorporating morphological and physiological aspects. Arch. Protistenkd. 128, 37–53. [https://doi.org/10.1016/S0003-9365\(84\)80027-5](https://doi.org/10.1016/S0003-9365(84)80027-5)

Pawlowicz R. 2013. Key physical variables in the ocean: temperature, salinity, and density. Nature Education Knowledge. 4, 13.

Peglar M.T., Amaral Zettler L.A., Anderson O.R., Nerad T.A., Gillevet P.M., Mullen T.E. et al. 2003. Two new small-subunit ribosomal RNA gene lineages within the subclass Gymnamoebia. J. Eukaryot. Microbiol. 50, 224–232. <https://doi.org/10.1111/j.1550-7408.2003.tb00122.x>

Penard E. 1890. Über einige neue oder wenig bekannte Protozoen. Jahrb. Nassau. Ver. Naturkd. 43, 73–91.

Penard E. 1902. Faune rhizopodique du bassin du Léman. Henry Kundig, Libraire de l'Institut, Geneva. <https://doi.org/10.5962/bhl.title.1711>

Perkins F.O. and Castagna M. 1971. Ultrastructure of the Nebenkörper or “secondary nucleus” of the parasitic amoeba *Paramoeba perniciosus* (Amoebida, Paramoebidae). J. Invert. Pathol. 17, 186–193. [https://doi.org/10.1016/0022-2011\(71\)90089-9](https://doi.org/10.1016/0022-2011(71)90089-9)

Pizzetti I., Schulz F., Tysl T., Fuchs B.M., Amann R., Horn M. et al. 2016. Chlamydial seasonal dynamics and isolation of ‘Candidatus *Neptuno-chlamydia vexilliferae*’ from a Tyrrhenian coastal

lake. Env. Microbiol. 18, 2405–2417. <https://doi.org/10.1111/1462-2920.13111>

Polne-Fuller M. 1987. A multinucleated marine amoeba which digests seaweeds. J. Protozool. 34, 59–165. <https://doi.org/10.1111/j.1550-7408.1987.tb03153.x>

Radir P.L. 1927. *Trichamoeba schaefferi*, a new species of large marine amoeba from Monterey Bay, California. Arch. Protistenkd. 59, 289–300.

Remane A 1934. Die Brackwasserfauna. Zool. Anz. 7 (Suppl), 34–74.

Rogerson A. 1991. On the abundance of marine naked amoebae on the surface of five species of macroalgae. FEMS Microbiol. Letters 85, 301–312. <https://doi.org/10.1111/j.1574-6968.1991.tb04756.x>

Rogerson A. 1993. *Parvamoeba rugata* n. g., n. sp. (Gymnamoebia, Thecamoebidae): an exceptionally small marine naked amoeba. Eur. J. Protistol. 29, 446–452. [https://doi.org/10.1016/S0932-4739\(11\)80407-4](https://doi.org/10.1016/S0932-4739(11)80407-4)

Rogerson A. and Gwaltney C. 2000. High numbers of naked amoebae in the planktonic waters of a mangrove stand in southern Florida, USA. J. Eukaryot. Microbiol. 47, 235–241. <https://doi.org/10.1111/j.1550-7408.2000.tb00042.x>

Rogerson A., Hannah F. and Gothe G. 1996. The grazing potential of some unusual marine benthic amoebae feeding on bacteria. Eur. J. Protistol. 32, 271–279. [https://doi.org/10.1016/S0932-4739\(96\)80026-5](https://doi.org/10.1016/S0932-4739(96)80026-5)

Rogerson A. and Hauer G. 2002. Naked amoebae (Protozoa) of the Salton Sea, California. Hydrobiologia 473, 161–177. https://doi.org/10.1007/978-94-017-3459-2_12

Rogerson A., Hannah F. J. and Anderson O. R. 1998. A redescription of *Rhabdamoeba marina*, an inconspicuous marine amoeba from benthic sediments. Invert. Biol. 117, 261–270. <https://doi.org/10.2307/3227028>

Rogerson A. and Laybourn-Parry J. 1992. The abundance of marine naked amoebae in the water column of the Clyde Estuary. Estuar. Coast. Shelf Sci. 34, 187–196. [https://doi.org/10.1016/S0272-7714\(05\)80104-0](https://doi.org/10.1016/S0272-7714(05)80104-0)

Rogerson A. and Patterson D. J. 2002. The naked ramicristate amoebae (Gymnamoebae). In: An illustrated guide to the protozoa, 2. Blackwell, Lawrence, pp. 1023–1052.

Ruinen J. and Baas Becking L.G.M. 1938. Rhizopods living in unusual environments. Arch. Néerland. Zool. 3, 181–198.

Sawyer T.K. 1971a. Isolation and identification

of free-living marine amoebae from upper Chesapeake Bay, Maryland. *Trans. Amer. Microsc. Soc.* 90, 43–51. <https://doi.org/10.2307/3224896>

Sawyer T.K. 1971b. *Acanthamoeba griffini*, a new species of marine amoeba. *J. Protozool.* 18, 650–654. <https://doi.org/10.1111/j.1550-7408.1971.tb03391.x>

Sawyer T.K. 1975a. Marine amoebae from surface waters of Chincoteague Bay, Virginia: two new genera and nine new species within the families Mayorellidae, Flabellulidae and Stereomyxidae. *Trans. Amer. Microsc. Soc.* 94, 71–92. <https://doi.org/10.2307/3225533>

Sawyer T.K. 1975b. Marine amoebae from surface waters of Chincoteague Bay, Virginia: one new genus and eleven new species within the families Thecamoebidae and Hyalodiscidae. *Trans. Amer. Microsc. Soc.* 94, 305–323. <https://doi.org/10.2307/3225496>

Sawyer T.K. 1975c. *Clydonella* n. g. (Amoebida: Thecamoebidae), proposed to provide an appropriate generic home for Schaeffer's marine species of *Rugipes*, *C. vivax* (Schaeffer, 1926) n. comb. *Trans. Amer. Microsc. Soc.* 94, 395–400. <https://doi.org/10.2307/3225504>

Sawyer T.K. 1980. Marine amoebae from clean and stressed bottom sediments of the Atlantic Ocean and Gulf of Mexico. *J. Protozool.* 27, 13–32. <https://doi.org/10.1111/j.1550-7408.1980.tb04225.x>

Sawyer T.K., Visvesvara G.S. and Harke B.A. 1977. Pathogenic amoebas from brackish and ocean sediments, with a description of *Acanthamoeba hatchetti*, n. sp. *Science*. 196, 1324–1325. <https://doi.org/10.1126/science.867031>

Schaeffer A.A. 1926. Taxonomy of the amoebas: with descriptions of thirty-nine new marine and freshwater species. Carnegie Inst. Washington, Washington.

Schaudinn F. 1896. Über den Zeugungskreis von *Paramoeba eilhardi* n. g. n. sp. *Sitz.-Ber. Kgl. Preuss. Akad. Wiss. Berlin* 14, 31–41.

Schaudinn F. 1899. Untersuchungen über den Generationswechsel von *Trichosphaerium sieboldi* Schn. *Abh. Preuss. Akad. Wiss., Berlin*, pp. 1–93.

Schmoller H. 1964. Beschreibung einiger Kulturamöben mariner Herkunft. *J. Protozool.* 11, 497–502. <https://doi.org/10.1111/j.1550-7408.1964.tb01787.x>

Schneider A. 1878. Beiträge zur Kenntnis der Protozoen. *Z. Wiss. Zool.* 30 (Suppl.), 446–456.

Schuler G.A. and Brown M.W. 2019. Description of *Armaparvus languidus* n. gen. n. sp. confirms

ultrastructural unity of Cutosea (Amoebozoa, Evosea). *J. Eukaryot. Microbiol.* 66, 158–166. <https://doi.org/10.1111/jeu.12640>

Schulz F., Tysl T., Pizzetti I., Dyková I., Fazi S., Kostka M. et al. 2015. Marine amoebae with cytoplasmic and perinuclear symbionts deeply branching in the Gammaproteobacteria. *Sci. Rep.* 5, 13381. <https://doi.org/10.1038/srep13381>

Schulze F.E. 1875. Rhizopodenstudien. *Arch. Mikr. Anat.* 11, 94–139. <https://doi.org/10.1007/BF02933791>

Sheehan R. and Banner F.T. 1973. *Trichosphaerium* – an extraordinary testate rhizopod from coastal waters. *Estuar. Coast. Mar. Sci.* 1, 245–260. [https://doi.org/10.1016/0302-3524\(73\)90038-8](https://doi.org/10.1016/0302-3524(73)90038-8)

Shmakova L., Bondarenko N. and Smirnov A. 2016. Viable species of *Flamella* (Amoebozoa: Variosea) isolated from ancient Arctic permafrost sediments. *Protist.* 167, 13–30. <https://doi.org/10.1016/j.protis.2015.11.001>

Sibbald S.J., Cenci U., Colp M., Eglit Y., O'Kelly C.J. and Archibald J.M. 2017. Diversity and evolution of *Paramoeba* spp. and their kinetoplastid endosymbionts. *J. Eukaryot. Microbiol.* 64, 598–607. <https://doi.org/10.1111/jeu.12394>

Sims G.P., Aitken R. and Rogerson A. 2002. Identification and phylogenetic analysis of morphologically similar naked amoebae using small subunit ribosomal RNA. *J. Eukaryot. Microbiol.* 49, 478–484. <https://doi.org/10.1111/j.1550-7408.2002.tb00232.x>

Sims G.P., Rogerson A. and Aitken R. 1999. Primary and secondary structure of the small-subunit ribosomal RNA of the naked, marine amoeba *Vannella anglica*: phylogenetic implications. *J. Mol. Evol.* 48, 740–749. <https://doi.org/10.1007/PL00006518>

Smirnov A.V. 1996. *Stygamoeba regulata* n. sp. (Rhizopoda) – a marine amoeba with an unusual combination of light-microscopical and ultrastructural features. *Arch. Protistenkd.* 146, 299–307. [https://doi.org/10.1016/S0003-9365\(96\)80017-0](https://doi.org/10.1016/S0003-9365(96)80017-0)

Smirnov A.V. 1997. Two new species of marine amoebae: *Hartmannella lobifera* n. sp. and *Korotnevella nivo* n. sp. (Lobosea, Gymnamoebida). *Arch. Protistenkd.* 147, 283–292. [https://doi.org/10.1016/S0003-9365\(97\)80055-3](https://doi.org/10.1016/S0003-9365(97)80055-3)

Smirnov A.V. 1999a. Re-description of *Thecamoeba munda* Schaeffer 1926 (Gymnamoebia, Thecamoebidae), isolated from the Baltic Sea. *Eur. J. Protistol.* 35, 66–69. [https://doi.org/10.1016/S0932-4739\(99\)80023-6](https://doi.org/10.1016/S0932-4739(99)80023-6)

- Smirnov A.V. 1999b. An illustrated survey of gymnamoebae isolated from anaerobic sediments of the Niva Bay (the Sound) (Rhizopoda, Lobosea). *Ophelia* 50, 113–148. <https://doi.org/10.1080/00785326.1999.10409392>
- Smirnov A.V. 2001. *Vannella ebro* n. sp. (Lobosea, Gymnamoebia), isolated from cyanobacterial mats in Spain. *Eur. J. Protistol.* 37, 147–153. <https://doi.org/10.1078/0932-4739-00811>
- Smirnov A.V. 2002. Re-description of *Vannella mira* Schaeffer 1926 (Gymnamoebia, Vannellidae), an often mentioned but poorly known amoebae species. *Protistology*. 2, 178–184. https://www.zin.ru/journals/protistology/num2_3/smirnov.pdf
- Smirnov A.V. 2003. Optimizing methods of the recovery of gymnamoebae from environmental samples: a test of ten popular enrichment media, with some observations on the development of cultures. *Protistology*. 3, 47–57. https://www.zin.ru/journals/protistology/num3_1/smirnov.pdf
- Smirnov A.V. 2007. Cryptic freshwater amoeba species in the bottom sediments of Nivå Bay (Øresund, Baltic Sea). *Eur. J. Protistol.* 43, 87–94. <https://doi.org/10.1016/j.ejop.2006.11.002>
- Smirnov A. 2009. Amoebas, Lobose. In: *Encyclopedia of microbiology*. Elsevier, Oxford, pp. 558–577. <https://doi.org/10.1016/B978-012373944-5.00359-X>
- Smirnov A.V. and Brown S. 2004. Guide to the methods of study and identification of soil gymnamoebae. *Protistology*. 3, 148–190. https://www.zin.ru/journals/protistology/num3_3/smirnov.pdf
- Smirnov A.V. and Kudryavtsev A.A. 2005. Pellitidae n. fam. (Lobosea, Gymnamoebia) – a new family, accommodating two amoebae with an unusual cell coat and an original mode of locomotion, *Pellita catalonica* n. g., n. sp. and *Pellita digitata* comb. nov. *Eur. J. Protistol.* 41, 257–267. <https://doi.org/10.1016/j.ejop.2005.05.002>
- Smirnov A.V., Nassonova E., Holzmann M. and Pawlowski J. 2002. Morphological, ecological and molecular studies of *Vannella simplex* Wohlfarth-Bottermann 1960 (Lobosea, Gymnamoebia), with a new diagnosis of this species. *Protist.* 153, 367–377. <https://doi.org/10.1078/14344610260450109>
- Smirnov A., Nassonova E., Berney C., Fahrni J., Bolivar I. and Pawlowski J. 2005. Molecular phylogeny and classification of the lobose amoebae. *Protist.* 156, 129–142. <https://doi.org/10.1016/j.protis.2005.06.002>
- Smirnov A.V., Nassonova E.S., Chao E. and Cavalier-Smith T. 2007. Phylogeny, evolution, and taxonomy of vannellid amoebae. *Protist.* 158, 295–324. <https://doi.org/10.1016/j.protis.2007.04.004>
- Smirnov A.V., Nassonova E.S. and Cavalier-Smith T. 2008. Correct identification of species makes the amoebozoan rRNA tree congruent with morphology for the order Leptomyxida Page 1987; with description of *Acramoeba dendroidea* n. g., n. sp., originally misidentified as ‘*Gephyramoeba* sp.’. *Eur. J. Protistol.* 44, 35–44. <https://doi.org/10.1016/j.ejop.2007.08.001>
- Smirnov A., Chao E., Nassonova E. and Cavalier-Smith T. 2011. A revised classification of naked lobose amoebae (Amoebozoa: Lobosa). *Protist.* 162, 545–570. <https://doi.org/10.1016/j.protis.2011.04.004>
- Smirnov A., Nassonova E., Geisen S., Bonkowski M., Kudryavtsev A., Berney C. et al. 2017. Phylogeny and systematics of leptomyxid amoebae (Amoebozoa, Tubulinea, Leptomyxida). *Protist.* 168, 220–252. <https://doi.org/10.1016/j.protis.2016.10.006>
- Sprague V. and Beckett R. L. 1966. A disease of blue crabs (*Callinectes sapidus*) in Maryland and Virginia. *J. Invert. Pathol.* 8, 287–289. [https://doi.org/10.1016/0022-2011\(66\)90156-x](https://doi.org/10.1016/0022-2011(66)90156-x)
- Sprague V. and Beckett R. L. 1968. The nature of the etiological agent of “gray crab” disease. *J. Invert. Pathol.* 11, 503–503. [https://doi.org/10.1016/0022-2011\(68\)90199-7](https://doi.org/10.1016/0022-2011(68)90199-7)
- Sprague V., Beckett R.L. and Sawyer T.K. 1969. A new species of *Paramoeba* (Amoebida, Paramoebidae) parasitic in the crab *Callinectes sapidus*. *J. Invert. Pathol.* 14, 167–174. [https://doi.org/10.1016/0022-2011\(69\)90103-7](https://doi.org/10.1016/0022-2011(69)90103-7)
- Stagg H.E.B., Hall M., Wallace I.S., Pert C.C., Garcia Perez S. et al. 2015. Detection of *Paramoeba perurans* in Scottish marine wild fish populations. *Bull. Eur. Assoc. Fish Pathol.* 35, 217–226.
- Stothard D.R., Schroeder-Diedrich J.M., Awwad M.H., Gast R.J., Ledee D.R., Rodriguez-Zaragoza S. et al. 1998. The evolutionary history of the genus *Acanthamoeba* and the identification of eight new 18S rRNA gene sequence types. *J. Eukaryot. Microbiol.* 45, 45–54. <https://doi.org/10.1111/j.1550-7408.1998.tb05068.x>
- Tanifuji G., Kim E., Onodera N. T., Gibeault R., Dlutek M., Cawthorn R. J. et al. 2011. Genomic characterization of *Neoparamoeba pemaquidensis* (Amoebozoa) and its kinetoplastid endosymbiont. *Eukaryot. Cell.* 10, 1143–1146. <https://doi.org/10.1128/EC.05027-11>
- Tanifuji G., Cenci U., Moog D., Dean S., Nakayama T., David V. et al. 2017. Genome sequencing reveals metabolic and cellular interdependence in an

amoeba-kinetoplastid symbiosis. *Sci. Rep.* 7, 11688. <https://doi.org/10.1038/s41598-017-11866-x>

Tekle Y.I., Grant J., Anderson O.R., Nerad T.A., Cole J.C., Patterson D.J. et al. 2008. Phylogenetic placement of diverse amoebae inferred from multigene analyses and assessment of clade stability within ‘Amoebozoa’ upon removal of varying rate classes of SSU-rDNA. *Mol. Phylogenet. Evol.* 47, 339–352. <https://doi.org/10.1016/j.ympev.2007.11.015>

Tekle Y.I. 2014. DNA barcoding in Amoebozoa and challenges: the example of *Cochliopodium*. *Protist.* 165, 473–484. <https://doi.org/10.1016/j.protis.2014.05.002>

Tekle Y.I., Anderson O.R., Katz L.A., Maurer-Alcala X.X., Romero M.A. and Molestina R. 2016. Phylogenomics of ‘Discosea’: a new molecular phylogenetic perspective on Amoebozoa with flat body forms. *Mol. Phylogenet. Evol.* 99, 144–154. <https://doi.org/10.1016/j.ympev.2016.03.029>

Tekle Y.I. and Wood F.C. 2017. *Longamoebia* is not monophyletic: phylogenomic and cytoskeleton analyses provide novel and well-resolved relationships of amoebozoan subclades. *Mol. Phylogenet. Evol.* 114, 249–260. <https://doi.org/10.1016/j.ympev.2017.06.019>

Tekle Y.I. and Wood F.C. 2018. A practical implementation of large transcriptomic data analysis to resolve cryptic species diversity problems in microbial eukaryotes. *BMC Evol. Biol.* 18, 170. <https://doi.org/10.1186/s12862-018-1283-1>

Telesh I.V., Schubert H. and Skarlato S.O. 2011. Revisiting Remane’s concept: evidence for plankton diversity and a protistan species maximum in the horohalimum of the Baltic Sea. *Mar. Ecol. Prog. Ser.* 421, 1–11. <https://doi.org/10.3354/meps08928>

Tymł T., Kostka M., Ditrich O. and Dyková I. 2016. *Vermistella arctica* n. sp. nominates the genus *Vermistella* as a candidate for taxon with bipolar distribution. *J. Eukaryot. Microbiol.* 63, 210–219. <https://doi.org/10.1111/jeu.12270>

Tymł T., Lisnerová M., Kostka M. and Dyková I. 2018. Current view on phylogeny within the genus *Flabellula* Schaeffer, 1926 (Amoebozoa: Lepatomyxida). *Eur. J. Protistol.* 64, 40–53. <https://doi.org/10.1016/j.ejop.2018.03.005>

Udalov I.A., Lee W.J., Lotonin K., Smirnov A. 2020a. *Pseudoparamoeba garorimi* n. sp., with notes on species distinctions within the genus. *J. Eukaryot. Microbiol.* 67, 132–139. <https://doi.org/10.1111/jeu.12763>

Udalov I.A., Lotonin K. and Volkova E. 2020b. Description of a new species of marine amoeba

Korotnevelia mutabilis n. sp. (Amoebozoa, Dactylopodida). *Eur. J. Protistol.* 75, 125701. <https://doi.org/10.1016/j.ejop.2020.125701>

Volkova E. and Kudryavtsev A. 2017. Description of *Neoparamoeba longipodia* n. sp. and a new strain of *Neoparamoeba aestuarina* (Page, 1970) (Amoebozoa, Dactylopodida) from deep-sea habitats. *Eur. J. Protistol.* 61, 107–121. <https://doi.org/10.1016/j.ejop.2017.09.006>

Volkova E., Völcker E., Claulß S., Bondarenko N. and Kudryavtsev A. 2019. *Paramoeba aparasomata* n. sp., a symbiont-free species, and its relative *Paramoeba karteshi* n. sp. (Amoebozoa, Dactylopodida). *Eur. J. Protistol.* 71, 125630. <https://doi.org/10.1016/j.ejop.2019.125630>

Volkova E. and Kudryavtsev A. 2021. A morphological and molecular reinvestigation of *Janickina pigmentifera* (Grassi, 1881) Chatton 1953 – an amoebozoan parasite of arrow-worms (Chaetognatha). *Int. J. Syst. Evol. Microbiol. Int. J. Syst. Evol. Microbiol.* 71(11):005094. <https://doi.org/10.1099/ijsem.0.005094>

Walochnik J., Haller-Schober E., Kolli H., Picher O., Obwaller A. and Aspöck H. 2000a. Discrimination between clinically relevant and non-relevant *Acanthamoeba* strains isolated from contact lens-wearing keratitis patients in Austria. *J. Clin. Microbiol.* 38, 3932–3936. <https://doi.org/10.1128/JCM.38.11.3932-3936.2000>

Walochnik J., Obwaller A. and Aspöck H. 2000b. Correlations between morphological, molecular biological, and physiological characteristics in clinical and nonclinical isolates of *Acanthamoeba* spp. *Appl. Environ. Microbiol.* 66, 4408–4413. <https://doi.org/10.1128/AEM.66.10.4408-4413.2000>

Walthall A.C., Brown M.W. and Tice A.K. 2016. A new species of *Flamella* (Amoebozoa, Variosea, Gracilipodida) isolated from a freshwater pool in Southern Mississippi, USA. *Acta Protozool.* 55, 111–117. <https://doi.org/10.4467/16890027AP.16.010.4945>

Wong F.Y., Carson J. and Elliott N.G. 2004. 18S ribosomal DNA-based PCR identification of *Neoparamoeba pemaquidensis*, the agent of amoebic gill disease in sea-farmed salmonids. *Dis. Aquat. Org.* 60, 65–76. <https://doi.org/10.3354/dao060065>

Young N.D., Crosbie P.B.B., Adams M.B., Nowak B.F. and Morrison R.N. 2007. *Neoparamoeba perurans* n. sp., an agent of amoebic gill disease of Atlantic salmon (*Salmo salar*). *Int. J. Parasitol.* 37, 1469–1481. <https://doi.org/10.1016/j.ijpara.2007.04.018>

Young N.D., Dyková I., Nowak B.F. and Mor-

rison R.N. 2008. Development of a diagnostic PCR to detect *Neoparamoeba perurans*, agent of amoebic gill disease. J. Fish Dis. 31, 285–295. <https://doi.org/10.1111/j.1365-2761.2008.00903.x>

Young N.D., Dyková I., Crosbie P.B., Wolf M., Morrison R.N., Bridle A.R. et al. 2014. Support for the coevolution of *Neoparamoeba* and their endosymbionts, *Perkinsela amoebae*-like organisms. Eur. J. Protistol. 50, 509–523. <https://doi.org/10.1016/j.ejop.2014.07.004>

Zlatogursky V.V., Kudryavtsev A., Udalov I.A., Bondarenko N., Pawlowski J. and Smirnov A. 2016. Genetic structure of a morphological species within the amoeba genus *Korotnevella* (Amoebozoa: Discosea), revealed by the analysis of two genes. Eur. J. Protistol. 56, 102–111. <https://doi.org/10.1016/j.ejop.2016.08.001>

Address for correspondence: Alexander Kudryavtsev. Laboratory of Cellular and Molecular Protistology, Zoological Institute of the Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 Saint-Petersburg, Russia; e-mail: alexander.kudryavtsev@zin.ru