

Review paper

A Half-century of Research on Free-living Amoebae (1965–2017): Review of Biogeographic, Ecological and Physiological Studies

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Abstract. This is a review of over 400 published research papers on free-living, non-testate amoebae during the approximate last half century (1965–2017) particularly focusing on three topics: Biogeography, Ecology, and Physiology. These topics were identified because of the substantial attention given to them during the course of the last half century, and due to their potential importance in issues of local and global expanse, such as: aquatic and terrestrial stability of habitats, ecosystem processes, biogeochemistry and climate change, and the role of eukaryotic microbes generally in ecosystem services. Moreover, there are close epistemological and thematic ties among the three topics, making a synthesis of the published research more systematic and productive. The number of reviewed publications for each of the three individual topics is presented to illustrate the trends in publication frequencies during the historical period of analysis. Overall, the number of total publications reviewed varied somewhat between 1965 and early 2000 (generally less than 10 per year), but increased to well over 10 per year after 2000. The number of Biogeography and Ecology studies identified in the online citations increased substantially after the mid 1990s, while studies focusing on Physiology were relatively more abundant in the first decade (1965–1974) and less were identified in the 1985 to 2004 period. Citations to the literature are listed in tables for each of the three topics for convenience in retrieving references to specific aspects, and representative examples of the cited research in the tables are reviewed in the text under subheads dedicated to each of the three topics. Biogeographic studies largely focused on the geographic distribution and localized patterns of occurrence of amoebae, with more recent studies incorporating more attention to likely correlates with environmental and biotic factors in the distribution and community composition of amoebae. Ecological studies reviewed in the later decades tended to focus more on community dynamics, the effects of environmental variables on communities (including climate-related topics), a trend toward more physiological ecology studies, combined field-based and experimental studies, and incorporation of newer methodologies such as molecular genetics. In general, physiology studies in the first decades of the review tended to focus on topics of cell physiology such as basic biochemistry, enzyme assays, mechanisms of cell division and development, encystment, and motility. Later studies examined broader topics such as osmoregulation, nutrition, fine structure evidence of cellular changes during the life cycle (including encystment and excystment), and issues related to asexual and sexual reproduction, with increasing substantial evidence of evolutionary patterns and phylogenetics based on molecular evidence. A final section on Conclusions and Recommendations summarizes the findings and presents some potentially productive approaches to future research studies on Amoebozoa within the three designated topics of analysis.

Key words: Amoebozoa, aquatic ecosystems, biogeography, ecology, environmental science, microbial physiology, terrestrial ecosystems, protistology

INTRODUCTION

This is a review of representative research on non-testate (naked) amoebae published during the recent half century (1965–2017), particularly focusing on three topics: 1) Biogeography, 2) Ecology, and 3) Physiology. Hereafter, I will use the term “amoeba” to mean naked, free-living amoebae, largely members of the Amoebozoa (previously “Gymnamoebia”), especially members of the lobose and filose groups, including (where appropriate) examples of the amoeboid stages of Heterolobosea and Myxomycete taxa when they particularly illustrate some of the breadth of research within each of the three designated topics. These three topics are chosen because they represent an interesting example of how amoeba research has developed over the recent approximate half century particularly in fields related to biogeography and physiological ecology.

This is an extensive, but not exhaustive, historically-based review intended to summarize some of the accomplishments in amoeba research within the three topics of Biogeography, Ecology and Physiology, with the aim of establishing a better documentation of the development of the field in the last half century, and more particularly suggesting some future directions that may be productive, especially if newer researchers in the field are seeking potential research topics to initiate or sustain their scholarly productivity. Also, amoebae have been studied less intensely than other eukaryotic microbes, and the increasing research, especially in ecology, is encouraging. Hopefully, this review may serve as a context for more intensive field-based and experimental research on amoebae. This is fundamentally a review, not a major, exhaustive summary of all published research on amoebae during the recent half-century. As such, I have had to make some judgments about what to include as “representative” of the publications during each decadal time period. However, as much as possible, I have tried to be representative in selecting examples of the total publications that were retrieved by an online search for each year, especially selecting examples that capture the broader range of the topics that were published. Therefore, the report of the number of published reports reviewed for each year (Fig. 1B–D) are only indicative of the trends in

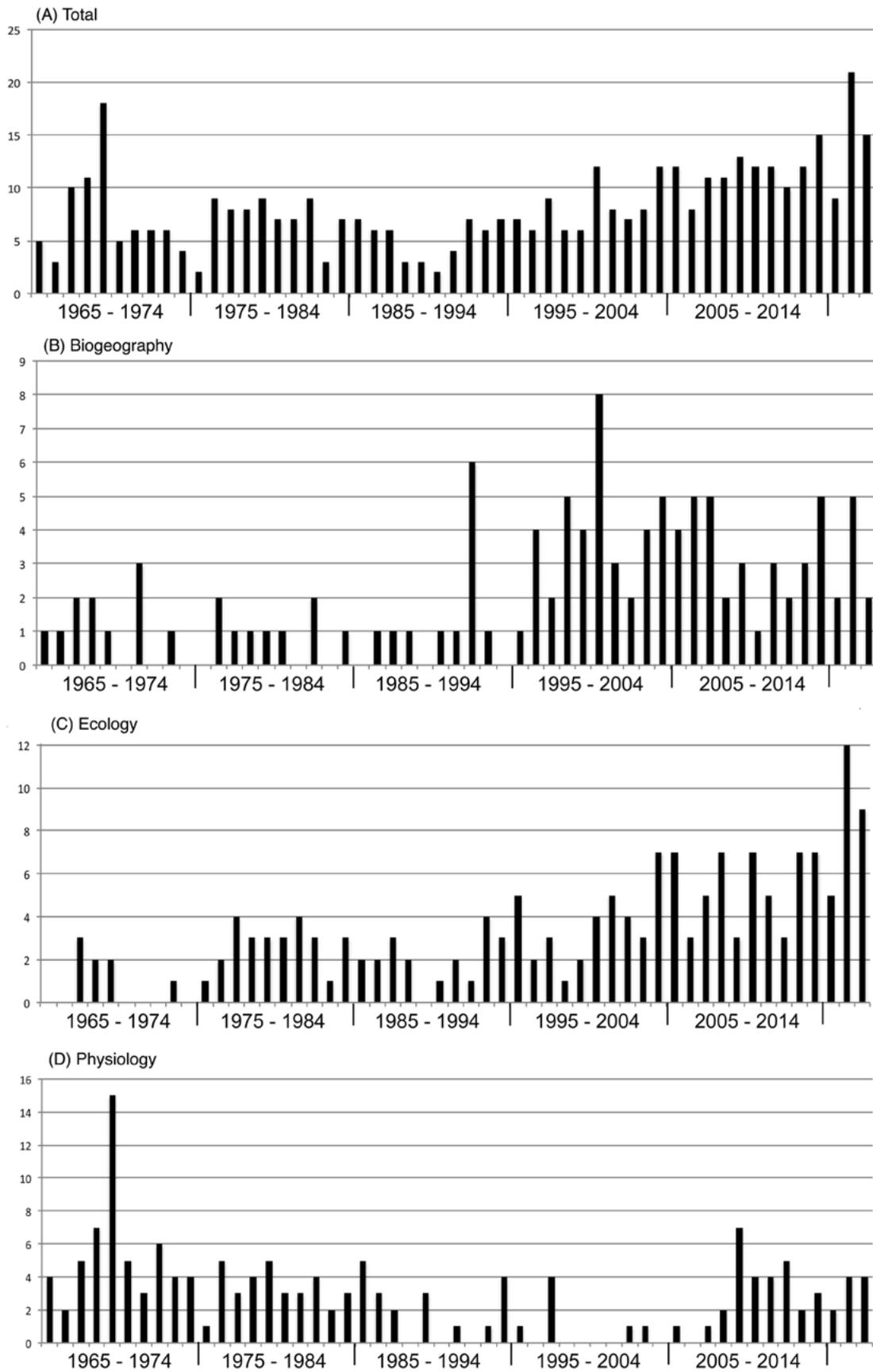
total publications, and should not be considered as a statistically-based assessment of the entire publications occurring each year.

The recent substantial research with amoebae (as with many protists), has deep historical origins extending back to at least the early nineteenth century, and before (e.g. Pritchard 1834). It is interesting to note that some of the research questions and themes that we continue to pursue in recent times have been of long-standing historical interest including such phenomena as locomotion, sensitivity to light and other stimuli, bacterial symbioses and feeding, etc. (e.g. Dellinger 1906; Leidy 1875, 1878; Mast 1910, 1926; Metcalf 1910). This is in addition to the substantial discoveries of classical morphologists and taxonomists (e.g. Rösel von Rosenhof, Leidy, Schaeffer, Schaudinn), extending into modern times (e.g. Bovee, Grell, Kudo, Page, Pussard, Sawyer, and others) that established a foundation for the modern advances in molecular phylogenetics of the field (e.g. Cavalier-Smith *et al.* 2015, Lahr *et al.* 2011, Pawlowski and Burki 2009, Smirnov *et al.* 2011, Tekle *et al.* 2008).

In preparing this review of amoeba research on the three stated topics during approximately fifty years, I chose to begin with the date of 1965, because it was a useful mid-decade starting point, and also provided a good reference point for the substantial research that emerged in the latter half of the twentieth century. In addition to the research contributions of many dedicated protistologists, we also have benefitted from the research on amoebae pursued by cellular physiologists (cum-protozoologists) who recognized that cultured amoeboid protists were good model systems for eukaryotic amoeboid cells in general, including the wandering cells of the mammalian cellular immune system and metastatic malignant cells, among other exemplars as cited in the section on Physiology of this review. Consequently, substantial research on the fundamental biochemistry and cellular physiology of cultured amoebae emerged during the latter half of the twentieth century, especially after axenic cultures of a few model amoebae were established, and before widely available axenic cultures of mammalian cells were developed. Some of these studies are included in this review in the section on Physiology.



Fig. 1A–D. Column graphs showing the number of published papers reviewed (ordinate) grouped by decades (abscissa). 1A – Total; 1B – Biogeography; 1C – Ecology; 1D – Physiology.



During a search of the literature using academic sources (e.g. *Google Scholar*, *Biosis*), I chose particularly the following key words: *amoeba* or *amoebae*, *gymnamoebae*, *naked amoebae*, and *free-living amoebae*. When information in identified sources also suggested using other search terms, these were included in additional searches to ensure that a reasonably good representation of research was covered during the designated historical period. The online search was further refined by examining each publication title and abstract to select citations most relevant to the three topics used in this review. If online versions of the published papers were not available, then only the abstract was used. However, for most cited items, it was possible to download a copy of the publication. Based on the title of an article, and an examination of the abstract and portions of the text, each collected item was assigned to one of the three review topics (Biogeochemistry, Ecology or Physiology) as plotted in column graphs (Figs. 1B–D). Publications that pertained to topics in biogeography or ecology were among those most challenging to categorize exclusively in only one of those two topics. However, as a guideline, those publications that included the word “biogeography” in the title were specifically placed in the category of Biogeography, when the content was clearly appropriate. Some other publications reporting new amoeba spp. collected from a particular geographic locale were generally placed within the topic of “Biogeography” to broaden the representative biogeographical publications covered in this review. Other research reports that dealt with clearly ecological research (autecology or synecology) going beyond sampling locale, to include broader ecosystems and community level studies, were grouped in the “Ecology” category. The Physiology category included research on biochemistry, cellular physiology, behavior, nutrition, etc. that clearly related to the basic science of amoeba cells, where less research attention was given to community or ecosystems level aspects.

All of the published citations reviewed have been listed in Summary Tables (Tables 1–6) within subcategories relevant to each topic to make the citations easily identified and their identification in the Reference section of this paper more accessible. There are two Summary Tables for each of the three major topics (hence six all-totaled), each one representing a major subtopic (e.g. Aquatic environments in one table, and Terrestrial environments in the other table). For example, citations for recovered articles on Biogeography appear in Summary Tables 1 and 2. Table 1 contains citations for

aquatic environments, and Table 2 for terrestrial environments. This was done to make each table more concise and readable, and also to make the listed citations to the references more easily identifiable. Because some recovered publications placed in Biogeography could also be useful in environmental and related research, the Biogeography entries (Tables 1 and 2) are further categorized in subcategories that may have environmental or ecological relevance (e.g. marine or freshwater locales, rivers and streams, soda lakes, terrestrial locales, grasslands, etc.). A few citations that appeared to be pertinent to two subcategories in the tables were listed in both table subcategories as a convenience to the reader who would prefer access to citations of interest across the categories.

No a-priori set of subcategories in each table was established in designing the Summary Tables; rather emergent subcategories were identified based on a review of the major foci of the papers within each of the broader three designated topic areas: Biogeography, Ecology, and Physiology. This is not intended to be a formal content analysis of the literature, but rather a review of some of the major themes that were pursued in research with amoebae over the previous half-century.

The next section, following this Introduction, presents a brief synopsis of the number of publications collected in total, and in addition for each of the three topic categories. After the synopsis section, there are three major sections, each representing a review of research corresponding to one of the three major topics (Biogeography, Ecology, and Physiology). The final section in this review is Conclusions and Recommendations.

Not all entries listed in the subsections of a respective Summary Table are reviewed in the text related to that section. Only some illustrative examples of the cited research are chosen from among the entries in each subsection of the Summary Tables to provide a perspective on the research. However, each Summary Table contains all citations listed in the Reference section that pertain to the subcategories in that Summary Table. Hopefully, the subcategorizations with their citations in each Table will enable the reader to find citations listed in the References that relate to a particular topic of interest.

Given the large number of references recovered in this review, the Reference section is subdivided into subsections, each corresponding to the major sections of the text (Introduction, Biogeography, Ecology and Physiology, including subdivisions corresponding to the titles of the pair of Tables for each of the three top-

ics). This is intended to make locating references cited in each of the sections (including those in the Tables) more convenient.

Additional information on various aspects of the biology of free-living amoebae (beyond this more detailed, historical perspective) can be found in Anderson (2017), Bradley and Marciano-Cabral (1996), Hauer and Rogerson (2005), Lei *et al.* (2014), and Rodriguez-Zaragoza (1994). There are also studies of opportunistic free-living amoebae that are medically important pathogens or parasites in addition to the important roles of amoebae in the natural environment. Some recent reviews of opportunistic amoebae include the following: Król-Turminska and Olender (2017), Schuster and Visvesvara (2004), Visvesvara (2010).

Some articles on relevant and emerging methods in biogeographic and ecology research include: Geisen and Bonkowski (2017), Beare *et al.* (1995), Behets *et al.* (2006), Douglas-Helders (2002), Fiore-Donno *et al.* (2016), Geisen *et al.* (2015), Kuiper *et al.* (2006), Rivière *et al.* (2006).

NUMERICAL SYNOPSIS OF RECOVERED PUBLICATIONS

The total number of recovered publications from the online search (1965–2017) was 431. The number recovered for each of the three topic categories was as follows: Biogeography (111), Ecology (171), and Physiology (149). The frequencies of recovered entries for each year, grouped by decades, are plotted as a bar graph, including total entries recovered (Fig. 1A), and for each of the topic categories: Biogeography (Fig. 1B), Ecology (Fig. 1C), and Physiology (Fig. 1D). With respect to the total entries recovered (Fig. 1A), there was a variable (but relatively low number < 10 per year) preceding the mid 1990s. However, during the first half of the 1965–1974 decade there was an upward trend with a peak at 18 entries in the year 1969, largely driven by a sharp increase in entries for Physiology (Fig. 1D). A further long-term upward trend occurred after 1995 reaching a peak of 21 in the year 2016, largely driven by a peak of 12 citations in the category of Ecology (Fig. 1C). Recovered entries for Biogeography were sparse prior to 1995 (with a mean of 1.5 per year) except for 1993 (peak of 6), with a mean of 1.5 per year; but the number increased substantially after 1995, with a mean of 3.5; and a peak of 8 in 2001. Recovered

entries for Ecology were variable, but more consistent in number (at four or less entries per year up to 1994), but showed a marked increase beginning about 2000, and rising to a peak value of 12 in 2016. By contrast, recovered entries for Physiology were most numerous in the period of 1965 to ~ 1985 (mean = 4.6 per year), with a slump after 1985 (with a few small peaks) until ~ 2010 when a comparable number per year as in 1965–1985 occurred (mean ~ 4.0).

BIOGEOGRAPHY

Recovered entries for Biogeography include two main subcategories Aquatic environments (Table 1) and Terrestrial environments (Table 2). Publications reviewed addressed polar, temperate and tropical biogeographic locales for both of these two ecosystem subcategories, with a much larger proportion devoted to temperate geographic locations. Overall, 14 entries addressed aquatic and terrestrial polar studies. Among these, Tyml *et al.* (2016) reported evidence of a new species of *Vermistella* from the Arctic, a genus previously collected only from the Antarctic (Moran *et al.* 2007); thus, this genus is at least bipolar.

Polar research. Three studies concerned amoebae from polar ice and melt water. Caron *et al.* (2017) reported the presence of naked amoebae grazing in sea ice habitats (a topic related to ecology as well), while Dillon *et al.* (1968) and Hada (1967) reported amoeba composition in Antarctic meltwater (and other locales). These include Antarctic isolates of *Amoeba alveolata* and *Trichamoeba clava* found by Hada (1967). Dillon *et al.* (1968) discovered a variety of non-testate amoeba in three families from locations on Ross Island. Shatlovich *et al.* (2009) and Shmakova *et al.* (2015) working in the Arctic recovered cysts of viable amoebae from permafrost with paleohistorical origins in the Late Pleistocene and Holocene. Although it is most likely that the frozen amoebae were encysted, recent evidence from temperate winter terrestrial samples indicates some nontestate amoebae can persist as non-encysted freeze-resistant stages in frozen soil (e.g. Anderson 2016, Bischoff and Connington, 2016; citations in Table 4: Terrestrial ecology, Temperate subsection). However, their survival rates while in a dormant state have not been determined beyond weeks to months.

Temperate research. Temperate aquatic studies addressed a broad range of topics encompassing reports

Table 1. Biogeography: Aquatic environments

Categories	Citations
<u>Polar</u>	
Marine	Mayes <i>et al.</i> (1998), Moran <i>et al.</i> (2007), Tong <i>et al.</i> (1997), Tysl <i>et al.</i> (2016)
Ice & melt water	Caron <i>et al.</i> (2017), Dillon <i>et al.</i> (1968), Hada (1967)
<u>Temperate</u>	
Aquatic general	Baumgartner <i>et al.</i> (2003), Niyati & Latifi (2017), Page (1971), Revill <i>et al.</i> (1967), Solgi <i>et al.</i> (2012)
Estuaries	Ettinger <i>et al.</i> (2003), Fernandez-Leborans <i>et al.</i> (2001), Juhl & Anderson (2014), Kiss <i>et al.</i> (2009), Muylaert <i>et al.</i> (2000)
Rivers & streams	Bovee (1965), Patcyuk & Dovgal (2012), Patsyuk (2014), Sleight <i>et al.</i> (1992)
Fresh water systems	Bell & Weithoff (2008), Lara <i>et al.</i> (2011), Smirnov & Goodkov (1996, 2004)
Coastal	Douglas-Helders <i>et al.</i> (2003), Fernandez-Leborans <i>et al.</i> (1999), Lighthart (1969), Munson (1992), Rogerson & Laybourn-Parry (1992), Sawyer (1971, 1990)
Marine algal surfaces	Armstrong <i>et al.</i> (2000), Rogerson (1991)
Open marine water	Davis <i>et al.</i> (1978), Murzov & Caron (1996), Vørs (1992)
Saline lakes	Davidson & Davidson (2005), Hauer <i>et al.</i> (2001), Rogerson & Hauer (2002),
Sediments	Burnett (1977), Butler & Rogerson (2000), Decamp <i>et al.</i> (1999), Kudryavtsev & Pawlowski (2013), Sawyer <i>et al.</i> (1992), Smirnov (2007), Smirnov & Thar (2003, 2004)
<u>Tropical</u>	
Lakes and lagoons	Amin <i>et al.</i> (2008), Bagatini <i>et al.</i> (2013), Finlay <i>et al.</i> (1987), Garstecki & Arndt (2000), Lugo <i>et al.</i> (1998)
Mangroves	Bhattacharya <i>et al.</i> (1987), Rogerson & Gwaltney (2000)

Table 2. Biogeography: Terrestrial environments

Categories	Citations
<u>Polar</u>	
Antarctic	Brown <i>et al.</i> (1982), Smith (1982, 1996), Wilkinson & Smith (2006)
Arctic	Shatilovich <i>et al.</i> (2009), Shmakova & Rivkina (2015), Tysl <i>et al.</i> (2016)
<u>Temperate</u>	
General & comparative	Bamforth (1984, 2004), Bischoff & Anderson (1998), Li <i>et al.</i> (2010), Ning & Shen (1998), Page (1976), Stephenson <i>et al.</i> (1993)
Grasslands or grassy sites	Anderson (2000), Bass & Bischoff (2001), Brown & Smirnov (2004), Geisen <i>et al.</i> (2014), Griffiths (2002), Rivera <i>et al.</i> (1992), Rogerson & Detwiler (1999)
Cave sediments	Garcia-Sanchez <i>et al.</i> (2013), Gittleson & Ferguson (1971), Walochnik & Mulec (2009)
Forests & woodlands	Feest & Madelin (1988), Mrva (2005), Old & Oros (1980), Timonen <i>et al.</i> (2004)
<u>Tropical</u>	
Arid land & deserts	Dumack <i>et al.</i> (2016), de Jonckheere <i>et al.</i> (2011), Mayzlish-Gati & Steinberger (2007), Rodriguez-Zaragoza & Garcia (1997), Rodriguez-Zaragoza <i>et al.</i> (2005)
Forests & wetlands	Amaral-Zettler <i>et al.</i> (2006), Bamforth (1976, 2007), Seneviratna & Waidyasekera (1995)

of amoeba assemblages from widely different ecosystems including freshwater (e.g. Bovee 1965, Bell and Weithoff 2008); coastal and estuarine (e.g. Douglas-Helders *et al.* 2003, Kiss *et al.* 2009, Rogerson and Laybourn-Parry 1991); and deep-sea sediments (e.g. Decamp *et al.* 1999, Sawyer *et al.* 1992, Smirnov 2007).

Fewer reports were recovered for tropical locales, and were largely from lakes, lagoons, and mangroves (e.g. Amin *et al.* 2008, Finlay *et al.* 1987, Bhattacharya *et al.* 1987).

Temperate terrestrial studies, some with ecological relevance, were done at grasslands and grassy sites.

Among other aspects these studies included the abundance, diversity and geographic distribution of amoebae (e.g. Brown and Smirnov 2004, Geisen *et al.* 2014, Griffiths 2002). Other temperate studies examined cave sediments (e.g. Gittleston and Ferguson 1971, Garcia-Sanchez *et al.* 2013), and soil in forests and woodlands (Feest and Madelin 1988, Old and Oros 1980). Additional temperate studies were of broader scope including desert locales and woodlands (e.g. Bamforth 1984, 2004), and comparative studies across broad geographic regions, e.g. Page (1976) who studied assemblages of amoebae in Britain and the U.S.A.

Tropical research. Tropical studies are grouped in two categories: Arid land and deserts (e.g. de Jonckheere *et al.* 2011, Dumack *et al.* 2016, Rodriguez-Zaragoza and Garcia 1997); and forests, woodlands, and wetlands. For example, Amaral-Zettler *et al.* (2006) reported recovery of an amoeba from tropical forest leaves; and Seneviratna and Waidyasekera (1995) reported the distribution of protists, including eight species of amoebae, in Sri Lankan wetlands.

ECOLOGY

Given the relatively large number of recovered published items, this category is subdivided into two large Divisions: Aquatic ecology (Table 3), and Terrestrial ecology (Table 4). There are some subcategories included in both of these tables, namely 1) biogeochemistry, 2) community interactions and dynamics, 3) trophodynamics and trophic interactions, and 4) various interactions of biota and the abiotic environment. Other subcategories, more specific to each of these divisions, are also included as shown in Tables 3 and 4.

Aquatic ecology

The aquatic ecology division is further subdivided into Freshwater and Marine sections (Table 3), with some subdivisions that are included in both of these subdivisions. Therefore, the citations reviewed here are addressed using topics from subsections that are present in both major divisions (Freshwater and Marine). However, the kind of water mass (freshwater or marine) is cited in the text to clarify which one is being referenced, beginning with Biofilms.

Biofilms in freshwater and marine environments. Biofilms are of increasing interest as hotspots of biological activity, and also as possible health hazards, because they can support a safe haven for pathogenic or-

ganisms, some of which are grazed on, or harbored, by amoebae. Biofilm research papers were found for both freshwater and marine environments. For example, Huws *et al.* (2005) examined the impact of protist grazing (including *Acanthamoeba castellanii*) on the population dynamics of freshwater bacteria in multispecies biofilm communities. *A. castellanii* has the capacity to graze on mixed biofilm communities and becomes integrally associated with them, whereas a ciliate was more destructive and reduced biofilm thickness by up to 60%. Parry (2004) published a substantial review of protozoan grazing of freshwater biofilms, with a specific section on amoebae. Anderson (2013) used Plexiglas plates as substrates in a northeastern U.S.A. freshwater pond, and reported data on amoeba densities, sizes, diversity and estimated C-biomass. Thirty morphospecies were identified, with large amoebae ($\geq 50 \mu\text{m}$) accounting for the greatest proportion of the C-biomass. Moreover, Johnson and Sieburth (1976) examined slime biofilms, obtained from a salmon marine hatchery, and reported that naked and scale-bearing amoebae, among other protists, formed a complex community with nitrifying-like bacteria. Smirnov (2001a, b) documented the diversity of amoebae in marine cyanobacterial mats grown in the laboratory after four years, and also isolated a relatively large new species (*Vannella ebro*) from cyanobacterial mats in Spain. He reported some of the physical environmental features tolerated by the new species.

Biogeochemistry. Biogeochemical studies were found largely in more recent publications, including a substantial review of the role of protozoa in aquatic nutrient cycles (Caron 1991), particularly with respect to ocean ecosystems. He also presented information on the role of amoebae and other protists in remineralization during surface dwelling on ocean aggregates. His research, and that of others, point out that our knowledge of the role of amoebae in ocean nutrient cycling is almost nil. Anderson (1997, 2007, 2016) has addressed the role of protists, including amoebae, in freshwater and marine C-cycles, including implications for global warming.

Community interactions including symbioses. Community interactions include a diverse array of studies in freshwater and marine environments, with a proportionally larger number of recovered studies for freshwater systems. For example, the presence of endosymbionts (particularly bacteria) in amoebae has been reported in studies ranging from the 1960s (Jeon and Lorch 1967) to recent reports in early twenty-first century. Dirren *et al.* (2014) reported the presence of ecto-

Table 3. Ecology: Aquatic environments

Categories	Citations
<u>Freshwater ecosystems</u>	
Biofilms	Anderson (2013), Huws <i>et al.</i> (2005), Parry (2004), Zubkov & Sleigh (1999)
Biogeochemical	Anderson (1997, 2007)
Community interactions	
Endosymbiosis	Dirren <i>et al.</i> (2014), Jeon & Lorch (1967), Jeon & Jeon (1976), Wang & Wu (2014), Yagita <i>et al.</i> (1995)
Structure & dynamics	Baldock <i>et al.</i> (1983), Bischoff & Horvath (2011), Bischoff & Wetmore (2009), Holt <i>et al.</i> (2002), Kusch (1993), Ramirez <i>et al.</i> (2010)
Plankton ecology	Ahmad (2009), Arndt (1993), Butler <i>et al.</i> (2000), Kiss <i>et al.</i> (2009), Urrutia-Cordero <i>et al.</i> (2013), Van Wichelen <i>et al.</i> (2016), Yamamoto (1981)
Environment seasonal	Khwon & Park (2017), Magnet <i>et al.</i> (2013), Mrva (2006), Xu <i>et al.</i> (2005)
Trophic interactions	
Algal predation	Canter (1973), Canter & Lund (1968), Smirnov <i>et al.</i> (2011)
Bacterial predation	de Moraes & Alkfiery (2008), Lawler & Morin (1993), Lesen <i>et al.</i> (2010)
Cyanobacterial predation	Ma <i>et al.</i> (2016), Van Wichelen <i>et al.</i> (2010), Wright <i>et al.</i> (1981), Xinyao <i>et al.</i> (2006)
Varied predation	Finlay <i>et al.</i> (1988), Kostomarova-Nikitina (1967), Salt (1968)
Water column processes	Anderson (2005), Anderson (2011), Oshima <i>et al.</i> (1986), Wörner <i>et al.</i> (2000)
<u>Marine ecosystems</u>	
Biofilms	Johnson & Sieburth (1976), Smirnov (1999, 2001a, b)
Biogeochemical	Caron (1991), Anderson (2016)
Community & abiotic interactions	Butler & Rogerson (1996), Davidson & Davidson (2005), Dyková <i>et al.</i> (2008), Mbugua (2008), Moss <i>et al.</i> (2001), Peglar <i>et al.</i> (2004)
Endosymbioses	Anderson (1977), Schulz <i>et al.</i> (2015)
Plankton ecology	Artolozaga <i>et al.</i> (1997), Caron <i>et al.</i> (1982), Mayes <i>et al.</i> (1998), Rogerson <i>et al.</i> (2003)
Salinity studies	Cowie & Hannah (2006), Hauer & Rogerson (2005), Lugo <i>et al.</i> (1998), Sawyer (2011)
Spatial & temporal variables	Anderson & Rogerson (1995), Butler & Rogerson (1995), Cowie & Hannah (2007), Fenchel (2010), Sawyer (1980)
Trophic interactions	Anderson (1994), Grell (1994), Laybourn-Parry <i>et al.</i> (1987), Polne-Fuller (1987), Rogerson & Hannah (1996), Rogerson <i>et al.</i> (1998)

and endosymbiotic bacteria associated with the amoeba *Nuclearia* sp. from lake Zurich. The ectosymbionts (several thousand cells) were regularly arranged inside a layer of extracellular polymeric substances produced by the amoeba on its surface; and endosymbionts (*Gammaproteobacteria*), with as many as 15–20 bacteria per amoeba, were enclosed in symbiosomes inside the host cytoplasm. The use of molecular genetic techniques has also provided new insights into amoeba-symbiont associations in freshwater (Wang and Wu 2014) and marine environments (e.g. Schulz *et al.* 2015). Transmission electron microscopy has provided new information on structural relationships of amoeba hosts and bacterial endosymbionts, for example non-membrane enclosed bacterial endosymbionts were reported in an *Acanthamoeba* sp. from the Philippines (Yagita *et al.* 1995). Similarly,

non-membrane enclosed bacteroids were also observed in electron microscopic sections of a marine mayorellid amoeba associated with blue-green algae (*Trichodesmium* tufts) in the Sargasso Sea (Anderson 1977).

Further community-based ecology studies have focused on interactions of amoebae with a wide variety of other biota, including chalk stream macrophytes (Baldock *et al.* 1985), zebra mussels in freshwater lakes (Bischoff *et al.* 2009), floating water hyacinth plants (Ramirez *et al.* 2010), marine ctenophores (Mbugua 2008, Moss *et al.* 2001), and interactions with invertebrates in the hypersaline Mono Lake (Davidson and Davidson 2005). Holt *et al.* (2002) studied the importance of biotic interactions in abundance-occupancy relationships, using *Amoeba proteus*, among other protists, to test experimentally whether interspecific in-

Table 4. Ecology: Terrestrial environments

Categories	Citations
Fundamental studies	
Biogeochemistry	Anderson (2008, 2012, 2014), Anderson & Griffin (2001), Anderson <i>et al.</i> (2017), Clarholm (1981), Coleman <i>et al.</i> (1977), Elliott <i>et al.</i> (1979, 1980), Gabilondo <i>et al.</i> (2015), Gould <i>et al.</i> (1979), Persson <i>et al.</i> (1980), Rønn <i>et al.</i> (2002), Zahn <i>et al.</i> (2016)
Community dynamics	
Plant interactions	Bonkowski (2004), Ekelund <i>et al.</i> (2009), Koller (2008), Krome <i>et al.</i> (2009), Laird (1966)
Microbe interactions	Bamforth (1988), Barrett (1977), Finlay <i>et al.</i> (2000), Jousset (2012), Neidig <i>et al.</i> (2010), Okafor (1966)
Endosymbionts	Denet <i>et al.</i> (2017), Greub <i>et al.</i> (2003), Horn & Wagner (2004)
Environmental variables	Andersen & Winding (2004), Anderson <i>et al.</i> (2001), Band (1995), Bryant <i>et al.</i> (1982), Cervero-Aragó <i>et al.</i> (2013), Cortés-Pérez <i>et al.</i> (2014), Darbyshire (2005), Ekelund <i>et al.</i> (2003), Grün <i>et al.</i> (2017), Stout (1984)
Trophodynamics	
Amoeba predation	Anderson & Patrick (1978), Danso <i>et al.</i> (1975), Murase & Frenzel (2008), Old & Darbyshire (1978)
Amoeba predators	Anderson <i>et al.</i> (1977–1978), Bonkowski & Schaefer (1997), Dreschler (1969), Elliott <i>et al.</i> (1980), Michel <i>et al.</i> (2014)
Worldwide ecosystems	
Alpine & polar	Anderson (2010), Anderson & McGuire (2013), Lin <i>et al.</i> (2017), Shatilovich (2009)
Desert	Darby (2008), Parker <i>et al.</i> (1984a, b), Rodriguez-Zaragoza <i>et al.</i> (2005, 2007)
Temperate	
Climate and seasons	Anderson (2004, 2016), Bischoff (2002), Rogerson (1982), Stout (1984)
Plant interactions	Amewowor & Madelin (1991), Bischoff & Connington (2016), Darbyshire & Greaves (1967), Darbyshire <i>et al.</i> (1977), Georgieva <i>et al.</i> (2005), Koller <i>et al.</i> (2013), Orosz <i>et al.</i> (2013), Weidner <i>et al.</i> (2017)
Soil biota interactions Soil environment	Dupont <i>et al.</i> (2016), Mrva (2005), Mulec <i>et al.</i> (2016), Qi <i>et al.</i> (2011), Weekers (1995)
Physical variables	Anderson (2002), Bryant <i>et al.</i> (1982), Geisen <i>et al.</i> (2014), Takenouchi <i>et al.</i> (2016), Vargas & Hattori (1990)
Chemical variables	Schnürer <i>et al.</i> (1985), Stapleton <i>et al.</i> (2005), Zhang <i>et al.</i> (2012)
Trophodynamics	Andriuzzi <i>et al.</i> (2016), Chakraborty <i>et al.</i> (1985), Geisen <i>et al.</i> (2016), Jahnke <i>et al.</i> (2007) Monroy <i>et al.</i> (2008)
Tropical	Liao <i>et al.</i> (2009), Seneviratna & Waidyasekera (1995)

teractions and dispersal influence the formation of the abundance–occupancy relationship in metapopulation systems in laboratory freshwater microcosms containing protists and bacteria. Abundance–occupancy relationships come about from the commonly observed pattern that abundance and distribution of species tend to be related, such that species declining in abundance often may also experience declines in the number of sites they occupy, while species increasing in abundance tend also to be increasing in occupancy. Holt *et al.* concluded that abundance–occupancy relationships in interacting communities were better defined than those in non-interacting communities.

Plankton ecology. Given the importance of plankton in the water column, the topic of plankton ecology is well represented among recovered publications

on amoebae, including freshwater studies in Antarctic lakes (Butler *et al.* 2000), and associations with cyanobacteria in other freshwater environments (e.g. Urrutia-Cordero 2013, Van Wichelen *et al.* 2016, Yamamoto 1981). Marine studies particularly are represented by the role of amoebae on suspended floc and marine snow in coastal locations, estuaries and open ocean (e.g. Anderson 2011, Artolozaga *et al.* 1997, Caron *et al.* 1982, Rogerson *et al.* 2003) emphasizing taxonomic composition, succession over time, and abundance on floc relative to surrounding water column. Mayes *et al.* (1998) presented one of the first studies to detail abundances of bacterivorous amoebae in East Antarctic coastal waters. They found, overall, numbers in the water column were highly variable (below detection to 2000 amoebae L⁻¹) and the data showed no clear seasonal trends.

Trophic relationships. Given the emphasis on relations with cyanobacteria reported in community studies, it is not surprising that trophic relationships included feeding on cyanobacteria in freshwater systems (Ma *et al.* 2016, Van Wichelen *et al.* 2010, Wright *et al.* 1981, Xinyao 2006) and marine environments (e.g. Laybourn-Parry *et al.* 1987). Predation has been reported on freshwater phytoplankton including centric diatoms (e.g. Canter 1973), and various algae (e.g. Canter and Lund 1968, Smirnov *et al.* 2011), including marine algae (Grell 1994, Polne-Fuller 1987, Rogerson *et al.* 1998), and other marine heterotrophic protists (e.g. Anderson 1994). In addition, as is more typical, heterotrophic bacterial predation was reported in aquatic ecosystems, including freshwater (e.g. de Moraes and Alfieri 2008, Lawler and Morin 1993) or in estuarine and marine environments (Lesen *et al.* 2010, Rogerson and Hannah 1996). Finlay *et al.* (1988) reported varied predation on cyanobacteria, bacteria and flagellates by ciliates in an African soda lake (Lake Nakuru). Kostomarova-Nikitina (1967) reported that the freshwater *Amoeba verrucosa* consumes nematode (*Ascaris*) eggs.

Water column interactions. A variety of more general water column interactions including interactions with other biota, seasonal and environmental interactions, and effects of chemical and physical variables have been reported. For example, some authors (e.g. Khwon and Park 2017, Magnet *et al.* 2013, Mrva 2006, Xu *et al.* 2005) reported environmental changes of amoebae and other protists in freshwater environments. Similar studies on changes in space and time in marine ecosystems were reported by Anderson and Rogerson (1995), Butler and Rogerson (1995), Cowie and Hannah (2007), Fenchel (2010), and Sawyer (1980).

Terrestrial ecology

Reviews of terrestrial ecology studies (Table 4) are reported in two major subcategories: “Fundamental studies,” not particularly related to any geographic place, and “World-wide studies” that are situated in various geographic locales. The Fundamental studies, therefore, are further subcategorized based on research focus (Biogeochemistry, Community dynamics, Environmental variables, and Trophodynamics). The World-wide ecosystem subcategory contains reviews further subcategorized based on ecosystems (e.g. Alpine and polar, Desert, Temperate, and Tropical).

Fundamental studies. Biogeochemical studies in soils particularly addressed nutrient remineralization, nutrient cycles, and the role of amoebae and other pro-

tists in fertility of the soil (e.g. Clarholm 1981, Coleman *et al.* 1977, Elliott *et al.* 1979, Zahn *et al.* 2016). With evidence of increasing atmospheric CO₂ concentrations, and its effects on the environment, more recent biogeochemical terrestrial studies focused on the effects of elevated CO₂ on amoeba associated protist communities and plants (e.g. Anderson and Griffin 2001, Gabilondo *et al.* 2015, Rønn *et al.* 2002). The significant role of eukaryotic terrestrial communities (including amoebae and other protists) serve in the global C-cycle and its importance for climate change has also attracted research interest (e.g. Anderson 2008, 2012, 2014, Anderson *et al.* 2017). Community dynamics relative to plant and amoeba interactions, included promoting plant growth and the microbial loop (Bonkowski 2004, Ekelund *et al.* 2009). An interesting study examined the protist community (including amoebae) in the aqueous suspension in the pitchers of pitcher plants (Laird 1969).

A variety of studies addressed some of the complex interactions of microbiota with each other in terrestrial environments. Finlay *et al.* (2000) employed a newer method for determining the potential abundance of free-living protozoa in soil. They reported that in diverse types of soil, flagellates were the most abundant, followed by naked amoebae, then the testate amoebae and ciliates, and noted that this order is inversely related to typical organism size in each group. Rogerson (1982) estimated the annual production and energy flow of large naked amoebae populations inhabiting a *Sphagnum* bog and reported that total consumption accounted for 361.0 kJ m⁻² yr⁻¹, of this 127.1 kJ was assimilated and 239.9 was egested. Moreover, of the assimilated energy, 77.4 kJ was respired.

At least 14 of the reviewed papers were concerned with interactions of amoebae with plants or specifically the plant rhizosphere. Studies examined the community structure and microbial interactions in the rhizosphere of plants, including the role of amoebae (e.g. Koller 2008, Krome *et al.* 2009), or in soil that had been altered by agriculture or addition of nutrients (e.g. Kramer *et al.* 2016, Schnürer *et al.* 1986, Stapleton *et al.* 2005, Zhang *et al.* 2012), or by effects of pollutants such as fuel oil spills (e.g. Anderson *et al.* 2001, Lara *et al.* 2007, Rogerson *et al.* 1981).

A number of studies addressed the effects of physical properties of soil on amoebae and other microbiota in soils, including drought and variability in water availability (e.g. Bischoff 2002, Bryant *et al.* 1982, Geisen *et al.* 2014, Stout 1984), oxygen tensions (e.g. Takenouchi 2016); and even possible effects on soil-

dwelling amoebae by stray, low-frequency, electromagnetic fields from communications antennas (Band 1995). This was part of an environmental monitoring survey, and no adverse effects were found.

Studies on trophodynamics examined amoeba predation in soils including feeding on fungi and methanotrophs as prey (e.g. Anderson and Patrick 1978, Danso *et al.* 1975, Murase and Frenzel 2008, Old and Darbyshire 1978). Likewise, predators on amoebae were studied, including nematodes, earthworms, and fungi as amoebophagous biota (e.g. Bonkowski and Schaefer 1997, Dreschler 1969, Elliott *et al.* 1980, Michel *et al.* 2014).

Worldwide ecosystems

As reported in prior major sections, research at temperate localities reviewed in this section was more substantially reported (30 entries) than for other global ecosystems. Among the range of studies in temperate regions, effects of climate and seasons were examined in protist ecosystems, including the role of amoebae (e.g. Anderson 2004, 2016, Bischoff 2002, Rogerson 1982, Stout 1984). Additional studies were done on amoeba and plant interactions within particular temperate locales. These included the role of decomposers in litter bags containing plant roots (e.g. Georgieva *et al.* 2005), remineralizing affordances of *Acanthamoeba* in the rhizosphere of maize and lucerne plants (Orosz *et al.* 2016), and stimulation of plant beneficial activity by pseudomonads in the presence of *Acanthamoeba* sp. (Weidner *et al.* 2017). *Acanthamoeba* and other free-living amoebae were examined in an extreme habitat with bat guano (Mulec *et al.* 2016), while Weekers *et al.* (1995) examined bacteriolytic activity of *Acanthamoeba castellanii*, *Acanthamoeba polyphaga*, and *Hartmannella vermiformis*, a group of free-living amoebae commonly found in terrestrial environments.

Several recovered temperate studies examined soil physical factors including soil particle size and granularity (e.g. Anderson 2002, Vargas and Hattori 1990), and chemical variables such as soil organic content (Schnürer *et al.* 1985, Zhan *et al.* 2012). Four reviewed publications examined temperate soil trophodynamics, such as the widespread occurrence of mycophagous amoebae (Geisen *et al.* 2016), and reduction in soil fungi due to mycophagous amoeba predation (Chakoborty *et al.* 1985). Monroy *et al.* (2008) documented changes in the density of amoebae and other biota in the gut of earthworms after ingestion, reporting that the densities of naked amoebae were substantially greater in the

gut samples of *L. rubellus* compared to the densities in the surrounding growth medium, suggesting that the amoebae were at least adaptable to the earthworm gut environment, and the gut-dwelling amoebae, if excreted, may be a reservoir for enrichment of the surrounding decomposition communities in the soil. Further evidence (Andriuzzi *et al.* 2016) indicates that the total abundance of protists and nematodes is only slightly higher in earthworm-occupied drilosphere compared to surrounding bulk soil, but strong positive effects were found for some protist clades (e.g. *Stenamoeba* spp.).

Some recovered studies examined the role of amoebae in alpine and polar terrestrial environments, with attention to factors such as respiration (Q_{10}), C-biomass, and protozoan grazing (e.g. Anderson 2010, Lin *et al.* 2017, Parker *et al.* 1984a, b, Rodriguez-Zaragoza *et al.* 2005, 2007). Desert studies, though fewer, addressed interesting topics such as ant nests and types of associated amoebae (Rodriguez-Zaragoza 2007), effects of rainfall and changes in C and N dynamics in litter communities (Parker *et al.* 1984a, b), or altered temperature and precipitation patterns on soil microbiota, and the role of amoebae in soil nutrient availability (Darby 2008).

Only two tropical site studies were recovered in the online survey, one was the study by Seneviratna and Waidyasekera (1995) on wetland protists in the Belanwila wetlands of Sri Lanka, and another by Liao *et al.* (2009) who studied soil sarcodina in Dongzhaigang mangroves, China.

PHYSIOLOGY

As reported in the Introduction, a substantial amount of fundamental biochemical and physiological research marked the early decades of research during this historical period, beginning in 1965 through 1985, with a second resurgence in activity in 2005–2017. Overall, given the large number of entries, the Physiology category is subdivided into two parts: 1) Cell biology, nutrition and symbioses, and 2) Locomotion, reproduction, life cycles and evolution. Table 5 contains citations to the first part on cell biology and related topics, and Table 6 contains citations for the second part on Locomotion and related topics.

Cell biology, nutrition and symbioses

There are two subsections for this topic (Table 5): 1) Cell physiology and 2) Nutrition. The first includes biochemical and fundamental cell biological topics,

Table 5. Physiology: Cell, nutrition, and symbioses

Categories	Citations
<u>Cell physiology</u>	
Biochemistry & enzymes	Barberá <i>et al.</i> (2010), Chapman-Andresen (1971), Halvey & Finkelstein (1965), Leger <i>et al.</i> (2013), Müller (1969a, b; 1985), Sopina (2003), Tomlinson (1967)
Cell size & energetics	Anderson (2006), Heal (1967), Nachmias (1986), Rogerson (1979, 1981), Rogerson <i>et al.</i> (1994), Wilkins & Thompson (1974)
Contractile vacuole & osmoregulation	Ahmad & Couillard (1974), Drainville & Gagnon (1973), Geoffrion and Larochelle (1984), Larochelle & Gagnon (1978), Lima <i>et al.</i> (2016), Pal (1972), Riddick (1968), Wigg <i>et al.</i> (1967)
Environmental effects	Chang (1991), Dolphin (1970), Landau (1965), Patsyuk (2013)
Respiration & anaerobiosis	Baldock <i>et al.</i> (1982), Cometa <i>et al.</i> (2011), Crawford <i>et al.</i> (1994), Prescott <i>et al.</i> (1974), Weik & John (1977)
<u>Nutrition</u>	
Consumption & growth	Adam & Blewett (1967), Bunt (1970), Butler & Rogerson (1997), Mayes <i>et al.</i> (1997), Pickup <i>et al.</i> (2007), Pigon (1970), Schuster (1979)
Feeding behavior	Cann (1986), Goodall & Thompson (1971), Kühn (1996/97), Old <i>et al.</i> (1985), Page (1977)
Phagocytosis & pinocytosis	Avery <i>et al.</i> (1995), Chattergee (1989), Christiansen & Marshall (1965), Hansson <i>et al.</i> (1968), Jeon & Jeon (1976), Josefsson (1968), Prusch & Hannafin (1979), Ryter & Bowers (1976), Schuster (1979)
Symbioses	Ahn & Jeon (1979), Delafont <i>et al.</i> (2015), Liu <i>et al.</i> (2011), Michel <i>et al.</i> (2010), Schulz <i>et al.</i> (2014), Whatley (1976)

Table 6. Physiology: Locomotion, Reproduction, Life cycle and Evolution

Categories	Citations
<u>Locomotion</u>	
Adhesion & chemotaxis	Brewer & Bell (1969), Grebecki (1982), Jahn <i>et al.</i> (1972), Jeon & Bell (1965), King <i>et al.</i> (1983), Lorch (1969), Klopocka & Stockem (1989), Martin (1987), McIntyre & Jenkin (1969), Nohmi & Tawada (1974), Pigon (1972)
Cytoskeleton	Allen R. D. (1972), Dembo (1989), Holberton (1969), Jones (1966), Taylor <i>et al.</i> (1973), Tekle & Williams (2017)
<u>Reproduction</u>	
Asexual reproduction	Feldherr (1968), Maciver (2016), Ord (1969), Rogerson (1980), Ron & Prescott (1969), Schuster (1975)
Sexual reproduction	Berney <i>et al.</i> (2015), Lahr <i>et al.</i> (2011), Röpstorff <i>et al.</i> (1993), Tekle <i>et al.</i> (2014, 2017), Tice <i>et al.</i> (2016)
<u>Life cycle & evolution</u>	
Encystment & excystment	Bowen <i>et al.</i> (1969), Fouque <i>et al.</i> (2012), Griffiths & Bowen (1969), Leitsch <i>et al.</i> (2010), Lloyd (2014), Martin & Byers (1976), Moon <i>et al.</i> (2012), Park <i>et al.</i> (2002), Pauls & Thompson (1981), Stevens & Pachler (1973), Sykes & Band (1985), Weisman <i>et al.</i> (1970)
Cell process	Akins <i>et al.</i> (1985), Band & Mohrlok (1969), Foque <i>et al.</i> (2014a), Griffiths & Hughes (1969), Lasman & Shafran (1978), Turner <i>et al.</i> (1997)
Cyst structure and control	Griffiths (1969), Lasman (1982), Lemgruber <i>et al.</i> (2010), Pasternak <i>et al.</i> (1970), Yang & Villemez (1994)
Excystment	Chambers & Thompson (1972), Datta (1979), Foque <i>et al.</i> (2014b), Stratford & Griffiths (1971)
Evolution and life cycles	Anderson (2010), Baldock & Berger (1984), Baldock <i>et al.</i> (1980), Cavalier-Smith <i>et al.</i> (2016), Kang <i>et al.</i> (2017), Przelecka & Sobota (1982), Tekle <i>et al.</i> (2008)

such as cell size, energetics, osmoregulation, respiration, and related environmental effects. The second on Nutrition, as the title implies, largely focuses on feeding behavior, feeding rates, food engulfment, and presence of symbionts that in some cases provide resources to the amoeba host.

Cell physiology. A substantial number of biochemical studies characterized the productivity in the early period of research in this historical analysis, including some major new discoveries such as the hydrogenosome (Müller 1985), and role of lysosomal enzymes and peroxisomes in cultured protists including amoebae (e.g.

Müller 1969a, b). Although evidence of hydrogenosomes has been reported in heterolobosean amoebae (e.g. Barberá *et al.* 2010), additional research is warranted to investigate possible evidence of hydrogenosomes in Amoebozoa, especially those dwelling in, or tolerant of, anaerobic environments, for example as in *Acanthamoeba* spp. (Leger *et al.* 2013).

Chapman-Andresen (1971) published a substantial review article on large amoebae including a section on “Some aspects of fine structure related to physiological processes;” and another appeared by Schuster (1979) on small amoebae and amoeboflagellates, with sections on cellular physiology, nutrition, growth, and encystment, among other topics. Because cell size, especially cell volume, is related to so many physiological processes, there was interest in improving the accuracy of estimating amoeba cell volume. Two methods were developed during this time. One expressed the cell volume in relation to the size of the stained nucleus (Rogerson *et al.* 1994), and another was based on a conversion factor relating the volume of a rounded-up amoeba to the length of the locomoting form, applicable to a broad range of different amoeba sizes and morphotypes (Anderson 2006). Amoeba cell volume has been used to estimate important variables such as respiration rate and amoeba total C-biomass (e.g. Anderson and McGuire 2013), although the accuracy of estimating C-biomass in amoebae and other protists is limited by the precision of the conversion factor used in converting cell volume to C-biomass units.

Several studies examined processes of new plasma membrane genesis essential for cell growth and some locomotory processes (e.g. Nachmias 1986, Wilkins and Thompson 1974), amoeba energetics (e.g. Rogerson 1981, Rogerson *et al.* 1994), and energy conversion efficiencies in amoebae (e.g. Heal 1967). Closely associated with energetics are issues of respiration rate assessed under defined conditions, and physiological responses to anaerobiosis. For example, several studies estimated respiration rate of protists including amoebae (Baldock *et al.* 1982, Crawford *et al.* 1994, Fenchel 2005) and others examined amoebae tolerance for low oxygen concentrations (Cometa *et al.* 2011). Likewise, to maintain respiratory carbohydrate metabolism in heterotrophic protists, carbon dioxide assimilation (anaplerotic fixation) is considered to be important, especially for maintenance of overall balance in carbon metabolism in metabolic pathways, including the tricarboxylic cycle. Among the enzymes mediating CO₂ heterotrophic C assimilation is phosphoenolpyruvate carboxylase

(PEP carboxylase). Prescott *et al.* (1974) examined the anaplerotic role of PEP carboxylase in *Acanthamoeba* and concluded that it had specific activity as high as that found for several tricarboxylic acid (TCA) cycle enzymes in this amoeba. This indicated a potential major role in sustaining C input into the TCA cycle from inorganic carbon, in addition to C sources derived from carbohydrate metabolism or other organic substrates.

Osmoregulation is physiologically linked to energetics, partially because energy is required to maintain osmotic balance, especially in freshwater environments where osmosis tends to drive excessive accumulation of water. Moreover, because some amoebae dwell in freshwater environments or in soil, where thin films of soil water are essential for active growth and feeding, the issue of osmoregulation was a topic of considerable interest (e.g. Drainville and Gagnon 1973, Geoffrion and Laroche 1984, Laroche and Gagnon 1978). Given the pivotal role of the contractile vacuole (CV) in osmotic regulation, several studies examined factors effecting CV activity, including temperature (Ahmad and Couillard 1974), output volume of CVs (Pal 1972), and CV internal content and mechanisms of function (Riddick 1968, Wigg *et al.* 1967). Environmental influences on cell form and function were also examined, such as the effects of high pressure on rounding up of amoebae (Landau 1965), and effects of light on enzymes and cell growth (Chang *et al.* 1991, Dolphin 1970).

Nutrition. This is a rather omnibus category, encompassing research on feeding rate and growth, behavior of feeding (phagocytosis), uptake of solutes (pinocytosis), and the role of symbionts that in some cases support host nutrition or otherwise promote metabolism. With respect to consumption rate in feeding and growth, studies were done in different geographic environments (e.g. Bunt 1970, Butler and Rogerson 1977, Mayes *et al.* 1997) as well as the effects of different culture media, nutrients and culture properties on the growth of amoebae (Adam and Blewett 1967, Pickup *et al.* 2007, Pigon 1970).

Feeding behavior (prey apprehension and engulfment) has been studied by electron microscopy (Goodall and Thompson 1971, Old *et al.* 1994); or by light microscopic evidence of feeding such as phagocytic consumption of centric diatoms (Kuhn 1996/97), and elaborate, prey-snaring cytoplasmic networks, as in *Synamoeba* during surface feeding on diatoms (Grell 1994). Mechanisms of phagocytosis were studied by several authors cited in Table 5 (e.g. Avery *et al.* 1995, Christiansen and Marshall 1965, Jeon and Jeon 1976);

including changes in digestive enzyme activity following phagocytosis (Ryter and Bowers 1976). Studies on pinocytosis included uptake processes (e.g. Chattergee 1989, Hanson *et al.* 1968), and the role of different cations on induction and inhibition of pinocytosis in *Amoeba proteus* (Josefsson 1968); and more specifically the role of external calcium ions in sucrose uptake (Prusch and Hannafin 1979).

A suite of studies by various authors examined the role of endosymbionts that were experimentally introduced in amoebae. These included a host-dependent bacterial endosymbiosis experimentally implemented over an extended period of time; eventually becoming permanent and indispensable to the host (Ahn and Jeon, 1979), and microinjection of zoochlorellae into *Amoeba proteus*, forming a “hybrid system” examined over time for changes in the physiological state of the amoeba, including the fate of the injected zoochlorellae (Liu *et al.* 2011). Other studies documented a host-specific, endocytic *Chlamydia*-like bacterium in *Saccamoeba limax* (Michel *et al.* 2010), the intracellular location of endobiont bacteria in *Pelomyxa* (Whatley 1976), as well as endobionts in some marine amoebae (Schulz *et al.* 2014), and evidence that a TM6 bacterium (previously only identifiable by DNA sequencing) was present and microscopically observed in *Vermamoeba vermiformis*, which incidentally resulted in inhibition of amoeba encystment (Delafont *et al.* 2015). More recently, three endosymbionts of *Pelomyxa palustris* have been shown to be prokaryotes (bacteria and methanogenic archaea), thus suggesting they may comprise a multipartite syntrophic consortium within the amoeba host cell, somewhat resembling similar syntrophic interactions found in complex microbial communities found in sewage treatment plant suspensions (Gutiérrez *et al.* 2017).

Locomotion, reproduction, life cycle and evolution

This part of the section on Physiology (Table 6) encompasses the three subtopics listed in the above sub-head. Locomotion particularly focuses on adhesion and chemotaxis with some references to cytoskeleton. Reproduction summarizes research on asexual reproduction in amoebae, and emerging evidence on the status of sexual reproduction based on experimental evidence. Life cycle and evolution has two main categories: Encystment and excystment, and Evolution and life cycles.

Locomotion. Several recovered publications dealt with amoeba attachment and locomotion (e.g. King *et al.* 1983, Lorch 1969, Martin 1987), while others were concerned with the mode of locomotion and its mecha-

nisms. For example, to elucidate extension of pseudopodia, Brewer and Bell (1969) studied the effects of ammonium ions on pseudopodium induction, while others such as Grebecki (1982) performed experimental studies to create models of how locomotion occurs. Studies on chemotaxis involved a variety of themes ranging from attraction of amoebae to prey, environmental influences on locomotion, and models of movement based on experimental analysis of cellular mechanisms. A variety of experiments were used to study how amoebae are attracted to prey, including use of fragments from potential prey (e.g. Jeon and Bell 1965), negatively charged proteins extracted from a ciliate potential prey (Nohmi and Tawada 1974), and documentation of prey and predatory activity by *Thecamoeba* spp. (Page 1977). Some studies examined environmental factors affecting locomotion such as temperature (Klopocka and Stockem 1989). Jahn *et al.* (1972) used a capillary suction test to evaluate the pressure gradient theory of amoeboid motion and reported that their results supported a “posterior contraction-hydraulic system” as opposed to a “frontal contraction system” that Allen (1972) had proposed based on evidence he had gathered from microscopic birefringence studies of cytoplasmic flow in amoebae.

It became clear very soon in cell biology studies that amoeba cytoplasm contains a cytoskeleton composed of subcellular, fine structural fibers and tubules, thus initiating several lines of investigation on the structure and function of the cytoskeleton. Among these were studies of the microtubules in amoebae (e.g. Holberton 1969), contractile proteins and their role in adhesion and locomotion (Jones 1966), elucidation of the cytoskeletal architecture and its implications for locomotion (Tekle and Williams 2017), and evidence for the mechanics and control of the cytoskeleton in amoebae (Dembo 1989).

Reproduction. Asexual reproduction by mitosis has been known from the earliest microscopic observations of amoebae that were maintained in laboratory cultures. However, details of mitosis remained enigmatic, but more recently have become elucidated with modern microscopic evidence including ultrastructure studies (e.g. Schuster 1975). Feldherr (1968), based on experimental studies of cross-transfer of nuclei between amoebae in different phases of mitosis, concluded that the breakdown of the nuclear envelope is not a result of some cytoplasmic constituent that signals or mediates the transformation, but rather it is a property of the nucleus itself, perhaps some co-occurring product

of intranuclear changes during late prophase to metaphase. Ord (1969) studied the control of DNA synthesis in *Amoeba proteus*, whereas Ron and Prescott (1969) studied the timing of DNA synthesis in *A. proteus*, and concluded that the S period occupies approximately the first 5–7 hours after onset of interphase for most cells, and that DNA synthesis begins sometime within the first 15 min. after cytokinesis. Studies at the organismic level (e.g. Rogerson 1980) examined factors affecting the generation times and reproductive rates in amoebae, including temperature and food concentration. Rogerson reported that temperature had a marked effect upon the generation times of *Amoeba proteus*, when cultured with *Tetrahymena pyriformis* as prey at temperatures of 20, 15, and 10°C. The length of the cell cycle varied from 44 hours at 20°C to 2926 hours at 10°C. Optimum reproductive rates were achieved at lower food levels as temperature was decreased.

An issue that has often perplexed the field of protistology is whether most amoebae are entirely asexual (e.g. Lahr *et al.* 2011) or if there are perhaps only rare sexual events that we fail to detect in laboratory studies. More recently evidence has emerged that extant amoebae were ancestrally sexual, but became largely asexual. Among other lines of evidence, Tekle *et al.* (2014) reported evidence of parasexual activity in laboratory-cultured amoebae based on microscopic observations of some peculiar cellular interactions in *Cochliopodium* spp. leading to multiple fusion of amoebae (plasmogamy) during laboratory culture. Plasmogamy is followed by nuclear fusions within the plasmodial-like fused cells producing enlarged nuclei with a mix of genetic content supplied from the fusing nuclei, this ultimately is followed by nuclear fission and cellular plasmotomy releasing daughter cells. It is very likely that the released daughter cells have nuclei with a new combination of chromosomal contents obtained during chromosomal mixing that occurs during multiple nuclear fusions. Moreover, Tekle *et al.* (2017) have presented molecular genetic evidence that amoebozoans are ancestrally sexual, based on the presence of sex genes and potential novel crossover pathways in diverse groups of extant amoebae. Other sources of evidence pointing toward an ancestral sexuality include studies on diverse life cycles in *Acanthamoeba*, thought to be entirely asexual (e.g. Tice *et al.* 2016); and evidence that amoeboid members of the Variosea fuse and can form cm-wide plasmodia (e.g. Berney *et al.* 2015).

Life cycle and evolution. A major feature of many protists, especially those in terrestrial and fresh water

environments (where moisture is sometimes unpredictable) is the process of encystment, i.e. the formation of a resting stage, usually enclosed by some type of protective organic envelope or wall. During the late 1960s, and thereafter, the biochemistry and molecular changes during encystment were of particular interest; for example, as reviewed by Lloyd (2014) for *Acanthamoeba*, and more broadly by Fouque *et al.* (2012) and references therein. A total of twelve studies were retrieved in the online search for the topic of encystment. Among the broad range of studies that emerged, the role of enzymes in encystment particularly attracted attention (e.g. Bowen *et al.* 1969, Leitsch *et al.* 2010, Martin and Byers 1976, Moon 2012, Sykes and Band 1985, Weisman *et al.* 1970), as well as changes in biologically significant macromolecules such as proteins (Park *et al.* 2002), unsaturated fatty acids (Pauls and Thompson 1981), RNA (Stevens and Pachler 1973), and glycogen (Weisman *et al.* 1970).

Cell processes during encystment occupied considerable attention across several decades of the time period reviewed here, including factors regulating encystment (Atkins *et al.* 1985), respiration during encystment (Band and Mohrlök 1969, Griffiths and Hughes 1969), effects of electrolytes and organic compounds on cyst formation (Lasman and Shafran 1978), and anaerobiosis induction of encystment in *Acanthamoeba castellanii* (Turner *et al.* 1997). As a natural sequel, research also examined cyst structure and its control during the process of encystment. For example, Lasman (1982) chronicled the cytoplasmic fine structure of cyst formation in *Acanthamoeba*, while Lemgruber *et al.* (2010) focused on the fine structure of the cyst wall. Pasternak *et al.* (1970) used scanning electron microscopy (SEM) to examine the changes in surface morphology of *Acanthamoeba* cells during laboratory-induced encystment. In a complementary study, Yang and Villemez (1994), using immunoanalysis techniques, reported that surface receptors in *Acanthamoeba* control its differentiation in both encystment and excystment. They reported that monoclonal antibodies that bind specifically to a 40 kD trophozoite surface protein initiate the encystment of the trophozoites, whereas when the antibodies are bound to cysts the same monoclonal antibodies prevent excystment. When the antibody is washed away, both trophozoites and cysts resumed normal activity. One of the monoclonal antibodies inhibits pinocytosis, while another has no effect on pinocytosis.

Further excystment studies, using SEM evidence, were reported by Chambers and Thompson (1972),

whereas other researchers examined the physiological changes including respiration and enzyme activities (Stratford and Griffiths 1971), and other studies examined the effects of organic and inorganic compounds, and CO₂ during excystment (e.g. Datta 1979).

A few studies on life cycles were recovered during this literature search. For example, Anderson (2010) in combined laboratory and field investigations examined the dynamics of encysted and trophic stages of naked amoebae using laboratory culture techniques to determine the ratio of active and encysted stages of amoebae collected from diverse terrestrial sites varying in plant cover, and moisture content during spring and summer months at a terrestrial site in N.E. U.S.A. The percentage of encysted amoebae varied between 32% and 100% depending on sampling locale and moisture content.

Additional evidence was gathered on the dynamic relationship that exists between active and encysted stages during emergence and proliferation of amoebae, with varying ratios depending on the moisture and physical qualities of the soil at the collection site. Baldock *et al.* (1980) reported laboratory growth rates of six species of freshwater amoebae at four different temperatures, and subsequently Baldock and Berger (1984) examined the effects of low temperatures on the growth of freshwater amoebae, and reported that generation times for cultures within a temperature range of 5.0 to 12.5°C were in the range of 19 hours to 178 hours, but decreased with increasing temperature. Minimum temperature for growth in three species fell below 5.0°C.

With respect to evolution, non-testate amoebae lack a substantial cell cover or envelope, hence they leave no discernible fossil record. Therefore, their evolution has not been studied as extensively as other protists, including test-bearing amoebae, with a fairly substantial fossil record. However, modern molecular phylogenetic methods have been applied to elucidate likely evolutionary patterns in non-testate amoebae (e.g. Cavalier-Smith *et al.* 2016, Kang *et al.* 2017, Tekle *et al.* 2008) resulting in an increasingly refined estimate of phylogenetic patterns for major groups of the Amoebozoa.

CONCLUSIONS AND RECOMMENDATIONS

The conclusions presented in this review (1965–2017) of published research on free-living, non-testate amoebae based on recovered citations using specific search words must be interpreted in the light of the ap-

proach that was used. The designation of three major topics of interest (Biogeography, Ecology, and Physiology), and a suite of related key words, established a context and boundary conditions for the kinds of citations retrieved during the approximately 50 years of history. However, during the online search, an earnest effort was made to follow-up with additional potential key words that emerged in some of the recovered publications to try to be as complete as possible. However, it is clear no search can be exhaustive, and some decisions had to be made about the relevance of some recovered texts to ensure a reasonable boundary on the number of citations included in this review. Nonetheless, a total of over 400 publications were recovered and plotted as a bar graph (Fig. 1A). Overall, during the earliest decades of the range of dates, a fairly consistent, though variable, number of publications were recovered from 1965 to approximately 1995. Thereafter, a substantial upward increase occurred exceeding 10 publications per year after 2004. Biogeography and Ecology publications (Fig. 1B, C) increased substantially after 1995, while the number of Physiology publications (Fig. 1D) tended to decrease at that date, but increased in frequency again at approximately 2005.

Biogeographic studies have been an important component of protist research, including studies specific to amoeboid taxa, particularly documenting the specific biogeographic locales of species, their geographic ranges, and diversity in varying ecosystems. There is an increasing amount of amoebozoan DNA sequence data in gene libraries, and coupled with modern high throughput sequencing of environmental samples, it should be possible to pursue a much more detailed analysis of the biogeographic distribution and community composition of amoebae across varied environments, globally based on environmental gene sampling. Furthermore, single-cell genomics may provide an important tool to better document the taxonomic identity of particular morphotypes sampled from varying geographic locales and, assuming they can be maintained in culture, provide the basis for more experimental studies on the environmental niches of amoebae and their adaptive capacity.

Alternatively, for isolates that cannot be cultured, RNA transcriptome studies using amoebae sampled directly from environmental microbial communities in varying locales, and dwelling in varied environmental conditions, may yield some insights into their state of metabolism and biological roles in a particular environment and at a given point in time. Additionally, transcriptome analyses of experimental laboratory studies

of bacteria and protist communities containing amoebae (where lab culturing is possible) can provide temporal evidence of the functional physiology of amoebae and other microbes as the dynamics of communities unfold over time.

The fundamental events in the life cycle of amoebae have been substantially documented, and additional research using modern molecular genetic techniques including transcriptome analyses may elucidate the metabolic changes that occur, and the details of cellular processes, during encystment and excystment. With recent emerging evidence that amoebae, previously assumed to be largely or totally asexual, may have ancestral sexual stages, it is of increasing importance to use modern genetic analytical methods to explore the genetic and developmental status of extant Amoebozoa taxa to establish their sexual characteristics in greater detail.

Some important biochemical and physiological findings were made during the early decades after 1965, especially in relation to fundamental cell processes documenting similarities of amoebae to other eukaryotic cells. At the same time, however, these studies also highlighted the unique biochemical and cellular events that marked the specialized adaptations of some free-living amoebae (e.g. encystment, specialized modes of nutrition, anaerobiosis, and mechanisms of locomotion). These studies, and those emerging in recent years on fundamental amoeba cellular processes, establish a strong foundation, in conjunction with modern ecological studies, to pursue a much more expanded research agenda on the physiological ecology of free-living amoebae in different geographic locales and particular habitats, especially in relation to changing climate and varied local environmental forcing functions.

This includes physiological autecology of particular amoebozoan taxa, and synecology of eukaryotic communities where free-living amoebae are present. More integrated field-based and laboratory studies are needed to better document the role of free-living amoebae in varied ecological settings; and combined with molecular genetic techniques may provide a much more detailed account of the bacteria taxa present in prokaryote-based, eukaryotic communities, as well as a more complete taxonomic accounting of the eukaryote microbes. Combined laboratory-based culture studies with molecular genetic techniques should yield a more refined and complete analysis of the varied roles of the prokaryotes and amoebae in microbial communities temporally, and in relation to changing environmental conditions.

One of the major ecological insights gained in the recent decades was the importance of water-column flocs and particulates in amoeba plankton dynamics. It has been known for a long time that amoeba must attach to a surface to locomote and feed. However, recent studies in freshwater and marine environments have more fully documented that amoeba abundance, diversity and localization depend on the quality and density of suspended matter in the water column. This has been particularly insightful in explaining the relative low abundance of amoebae in some open ocean locations where insufficient suspended substrate is available. However, it also opened a productive field of inquiry on the role of amoebae in “marine snow” flocs both suspended in the water column and settling at depth in open ocean locations.

Additional systematic field-based and laboratory research is needed to more fully examine the structure and dynamics of amoeba-containing microbial communities on floc surfaces suspended in the water column in various aquatic environments (freshwater to marine). Among other potential topics, the successional stages that occur when excysting amoebae attach to, and begin to proliferate on, bacterial-containing floc needs to be more fully documented; especially in relation to ensuing changes in the prokaryote and amoeba populations, as well as the variations in biomass among the constituent taxa inhabiting the floc over time. These studies, moreover, may be productively pursued in relation to changes in the physical and chemical characteristics of the water column (e.g. salinity, inorganic and organic nutrient loads of varying composition, temperature, water quality including presence or absence of pollutants, and oxygen concentrations, etc.).

Syntrophy has become one of the major topics of research in natural prokaryote communities, and further extension of these studies to examine the possible role of amoebozoa as syntrophs within amoeba assemblages in microbial communities, and with the prokaryotes in these mixed microbial communities, may be an increasingly productive line of inquiry. The particular metabolic roles of ecto- and endobacterial symbionts in amoebae may also contribute to interactions in syntrophic metabolic networks of mixed bacterial and protist communities. This includes communities on flocs suspended in the water column, on surfaces in sediments and other solid surfaces, and on particulates and pore spaces in soil environments. Research on amoeba-containing biofilm communities has been somewhat limited, but some of the above-mentioned research strategies may

be extended to include biofilm physiological ecology in freshwater and marine environments.

Current biogeochemical studies of amoeba-containing microbial communities are limited, and it is important to clarify the potential role of free-living amoebae in biogeochemical cycles. On the whole, amoebae typically may not constitute a major component of the total ecosystem microbial biomass, but their importance in trophodynamics, and capacity to alter the physical and chemical environment (locally or more extensively) within micro domains where these microbial communities are found, may have greater impact on biogeochemical cycles than realized here-to-fore. Through their alterations of the bacterial composition during predation, and release of nutrients during phagotrophy or excretion of wastes, amoebae may have important forcing functions on the biogeochemistry of aquatic and terrestrial ecosystems. With increasing evidence that the activity of protists at the very base of eukaryotic microbial communities may have effects that extend beyond local ecosystems to global levels, additional research on all aspects of the contributions of prokaryotes and eukaryotic microbes to natural environmental processes is increasingly important.

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