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Protistology

Review

Taxonomy of amoeboid protists: a brief history of research from C. Gessner to T. Cavalier-Smith

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Summary

Amoeboid protists are characterized by presence of pseudopodia of different types (lobopodia, filopodia, reticulopodia and axopodia) and have been known for researchers since the ancient times. The taxonomic system of amoeboid protists dramatically changed during the history, especially since the development of molecular phylogenetic approaches. Many taxa widely used in the 19th century are now considered invalid and artificial. The existent reviews usually focuse only on the modern period of time or, on the opposite, on early classifications with some key works omitted. In this review, I focused on the evolution of views on the amoeboid protists' systems and highlighted the most important works from the first mention of amoeboid protists until the present day.

Key words: amoeboid protists; history of amoeboid protists; history of science; protistology; protists

Ancient history

Amoeboid protists were first described in ancient times by Herodotus (5th century BC) who noticed nummulites (shells of macroscopic Foraminifera) in the stone of Egyptian pyramids (after Pokorný, 2015). In the 1st century BC and AD, foraminiferans were observed by Strabo and Pliny (after Pokorný, 2015). Much later, C. Gessner (1565) described one of the species of foraminifera. Like his antique predecessors, Gessner made observations with the naked eye. Starting from R. Hooke (1665), all descriptions of amoeboid protists (e.g., Joblot, 1718; Rösel von Rosenhof, 1755; Eichhorn, 1783; Müller, 1786; Leclerc, 1815) were made using a light microscope. One of the most prominent works of that period was A. d'Orbigny's monograph (1826), where the author placed microscopic "cephalopods" that lacked a siphon into the order Foraminifera.

The 19th and 20th centuries. First systematics of amoeboid protists

Probably the first attempt to classify amoeboid protists was made by C.G. Ehrenberg (1838). In his monograph "Die Infusionsthierchen als vollkommene Organismen" ("Infusoria as ideal organisms") he divided the so-called "stomach animals" (Magenthiere) into two groups: Stomachlless

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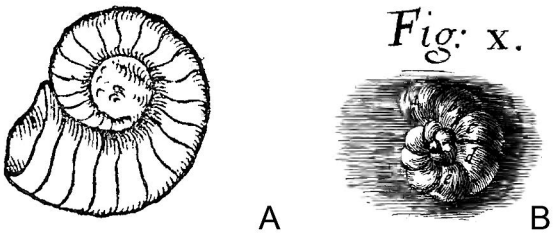


Fig. 1. A –"Hammonis cornu" by C. Gessner (1565); B – Rotaliform foraminifera by R. Hooke (1665).

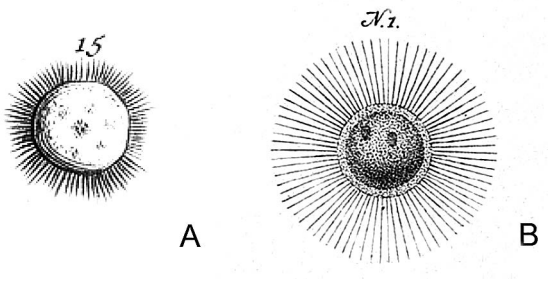


Fig. 2. A – "An extraordinary fish" (heliozoan of uncertain taxonomic affinity) by L. Joblot (1718); B – "The star" (*Actinosphaerium* sp.) by J.C. Eichhorn (1783).

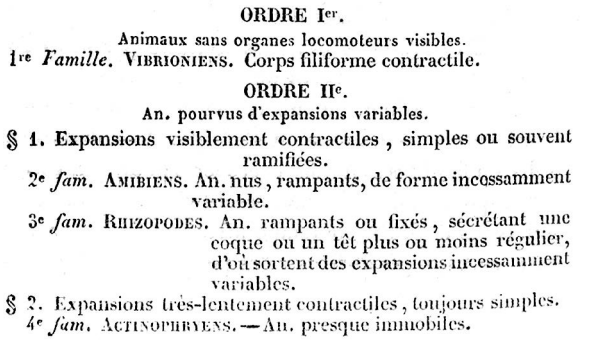
(Darmlose, Anentera) and Stomachic (Darmführende, Enterodela). The first group included the section Pseudopoda (Wechselfüssige, Pseudopoda), which combined the families Amoebaea and Arcellina, freshwater naked and testate lobose amoebae that were divided according to the absence or presence of a shell. Despite the establishing of several genera and description of a number of species that are still valid nowadays, Ehrenberg erroneously considered all unicellular "infusoria" as "ideal" and having the organization similar to multicellular creatures. Thus, among other characters, he described their mouths, "complex stomachs", esophagus, anus and other organs.

Even before publication of Ehrenberg's work, on January 23, 1835, F. Dujardin made a presentation where he stated that so-called "microscopic cephalopods" are actually not cephalopods at all and proposed for them a new name "symplectomères". He made this report at the one of first meetings of the Société des Sciences Naturelles de France. The same year, in late June, Dujardin sent letters to the Académie des Sciences and to a scientific newspaper, "L'Institut". In those letters, he proposed a new name for his "symplectomères" — "rhizopodes" (from the Greek "ῥίζα" — root and "πούς" — foot). According to Dujardin, these organisms had branching cell projections or feet, used for both motility and prey capture, that resembled roots (after Dolan, 2021). In 1835, Dujardin also introduced the term "sarcode" (from the Greek "σάρξ" — muscle tissue, flesh and "εἶδος" — similar) for a jelly-like, granular substance capable of stretching itself into long threads of which the body

Uebersicht der 22 Familien der Magenthiere:

Darmlose, *Anentera:*	Anhanglose (Fusslose), *Gymnica:*	Körperform beständig	vollkommene Selbsttheilung	panzerlose	**Monadina**
				gepanzerte	**Cryptomonadina**
			unvollkommene Selbsttheilung (Monadenstockbildung)	allseitige Selbsttheilung, mit Panzer (Kugelbildung)	**Volvocina**
				einseitige Selbsttheilung (Fadenbildung) panzerlose	**Vibrionia**
				einseitige Selbsttheilung (Fadenbildung) gepanzerte	**Closterina**
		Körperform wechselnd	panzerlose		**Astasiaea**
			gepanzerte		**Dinobryina**
	Wechselfüssige, *Pseudopoda:*	panzerlose			**Amoebaea**
		gepanzerte		vieltheiliger Fuss aus einzelner Oeffnung	**Arcellina**
				einfacher Fuss aus einzelner oder jeder einzelnen Oeffnung	**Bacillaria**
	Behaarte, *Epitricha:*	panzerlose			**Cyclidina**
		gepanzerte			**Peridinaea**
Darmführende, *Enterodela:*	Einmündige, *Anopisthia:*	panzerlose			**Vorticellina**
		gepanzerte			**Ophrydina**
	Gegenmündige, *Enantiotreta:*	panzerlose			**Enchelia**
		gepanzerte			**Colepina**
	Wechselmündige, *Allotreta:*	panzerlose		mit von einem Rüssel überragten Munde ohne Schwanz	**Trachelina**
				mit vorderem Munde und schwanzartigem Bauchende	**Ophryocercina**
		gepanzerte			**Aspidiscina**
	Bauchmündige, *Catotreta:*	panzerlose		nur mit Wimpern bewegt	**Colpodea**
				mit mehrfachen Bewegungsorganen	**Oxytrichina**
		gepanzerte			**Euplota**

Fig. 3. System of "Infusoria" of C.G. Ehrenberg (1838).



ORDRE Ier.

Animaux sans organes locomoteurs visibles.

1re *Famille.* VIBRIONIENS. Corps filiforme contractile.

ORDRE IIe.

An. pourvus d'expansions variables.

§ 1. Expansions visiblement contractiles, simples ou souvent ramifiées.

2e *fam.* AMIBIENS. An. nus, rampants, de forme incessamment variable.

3e *fam.* RHIZOPODES. An. rampants ou fixés, sécrétant une coque ou un têt plus ou moins régulier, d'où sortent des expansions incessamment variables.

§ 2. Expansions très-lentement contractiles, toujours simples.

4e *fam.* ACTINOPHRYENS. — An. presque immobiles.

Fig. 4. System of F. Dujardin (1841).

of foraminifera, as well as testate and naked lobose amoebae, consisted. Dujardin observed contraction and crawling movement of a "sarcode" and found granules inside it, but no presence of any organs (after Carter, 1852 and Dolan, 2021).

In 1841, Dujardin (1841) suggested his classification of amoeboid organisms, which included naked and testate lobose amoebae, foraminifera and actinophryid heliozoans.

He united them into one unnamed order (ordre IIe) with the diagnosis "infusoires pourvus d'expansions variables" ("infusoria with various outgrowths"). The order was subdivided into three families: Amibiens, Rhizopodes and Actinophryens. The taxon Rhizopodes, despite its name, did not include protists with root-like branched pseudopodia, but embraced the shelled ones. Thus, the lobose testate amoebae *Difflugia* and *Arcella*, lacking rhizopodial pseudopodia, also got therein. Naked lobose amoebae were assigned to the first group, and actinophryid heliozoans were placed in the third. The latter were separated from the two previous groups based on the presence of long, contractile and unbranched pseudopodia. Since the publication of Dujardin's monograph in 1841, the name "Rhizopoda" has become widely used by researchers, but in a very different way.

M. Schulze (1854) followed Dujardin and divided amoeboid protists to naked and shelled ones, but introduced his own names for these groups. Thus, the genus Amoeba fell into the first group Nuda, that is, "naked". For shelled rhizopods, he first suggested the name "Testacea", that is, "shelled". Last group was synonymous with Dujardin's Rhizopodes, but was subdivided into Monothalamia (forms with a single chambered shell: rhizopods with lobose, filose, and reticulose pseudopodia) and Polythalamia (multi-chambered foraminiferans).

J.P. Müller (1858) used another principle for his classification and divided all rhizopods by presence or absence of contractile vacuoles, thus separating freshwater and marine representatives. He also was the first to notice the similarity between Polycystina and *Thalassicolla* described earlier by Ehrenberg (1839) and by H. Huxley (1851), respectively, and *Acanthometra* that Müller (1855) had described previously. Müller grouped Acantharia, Polycystina and *Thalassicolla* into one group, which he called "Rhizopoda radiaria" or "Radiolaria" (from the Latin "radiolus", "ray"), considering all these organisms to be closely related to all other rhizopods. Nonetheless, Müller erroneously assumed that representatives of *Thalassicolla* could be close to sponges because both groups of organisms produce siliceous spicules. Thus, the first group, Infusoria rhizopoda, included all freshwater rhizopods (lobose naked and testate amoebae, filose testate amoebae, and heliozoan *Actinophrys*), and the second, Rhizopoda genuine, included all marine representatives (Polythalamia, that is, Foraminifera, and Radiolaria). He separated foraminiferans and radiolarians according to the chemical composition of the shell and its shape. The former had a calcium or organic shell and the latter had a silicon radial skeleton.

É. Claparède and J. Lachmann (1858) followed Müller in the basal division of rhizopodes to freshwater (with contractile vacuole) and marine (lacking this organelle), but named Müller's "Infusoria rhizopoda" as order "Proteina" and listed marine rhizopods without grouping as representatives of three orders: Echinocystida (Müller's Radiolaria), Gromida and Foraminifera. They also drew attention to the structure of the pseudopodia and noted the similarity of broad pseudopodia of naked lobose and testate amoebae, anastomosing pseudopodia of Gromida and Foraminifera and thin tapering ones in Actinophryna and Echinocystida.

Being the student of J.P. Müller, E. Haeckel worked mostly on radiolarians. In his first work on this topic (Haeckel, 1860), he described in detail the structure of the soft part of radiolarians' bodies. According to his studies they consisted of a central capsule, through which a huge number of rigid filamentous pseudopodia emerge. Depending on the family, the skeleton might surround the central capsule (as in solitary Polycystina) or penetrate inside the capsule (as in Acanthometra or colonial polycystins) (after Richards, 2008). Despite the

1. Schultzes System.

A. NUDA. Ohne Gehäuse. Gattung: *Amoeba*.

B. TESTACEA. Mit Gehäuse.

I. **Monothalamia.** Gehäuse einkammerig, das Thier ungetheilt.

1. Lagynida. Eine beutelförmige, kalkige oder membranöse, nicht fein poröse Schale, mit einer grossen Oeffnung. Gattungen: *Arcella, Difflugia, Trinema, Euglypha, Gromia, Lagynis, Ovulina, Fissurina, Squamulina.*
2. Orbulinida. Eine kugelige, kalkige Schale ohne grössere Oeffnung, an der ganzen Oberfläche fein durchbohrt. Gattung: *Orbulina.*
3. Cornuspirida. Eine kalkige Schale, wie ein Planorbisgehäuse gewunden, mit einer grossen Oeffnung. Gattung: *Cornuspira.*

II. **Polythalamia.** Gehäuse vielkammerig, das Thier aus zusammenhängenden Segmenten gebildet.

1. Rhabdoidea (*Nodosarida* sive *Stichostegia*).
2. Helicoidea (*a. Miliolida. b. Turbinoida. c. Nautiloida. d. Alveolinida. e. Soritida*).
3. Soroidea. *Acervulinida.* Gattung: *Acervulina.*

Fig. 5. System of M. Shulze, 1854 (from Haeckel, 1862).

2. Müllers System.

A. INFUSORIA RHIZOPODA. Mit contractiler Blase. Gattungen: *Amoeba, Arcella, Difflugia, Trinema, Euglypha, Actinophrys.*

B. RHIZOPODA GENUINA. Ohne contractile Blase.

I. **Polythalamia.** Gehäuse kalkig oder membranös. Typus nur ausnahmsweis radiär, meist spiral.

II. **Radiolaria.** Skelet fehlend oder kiesclig. Typus constant radiär, niemals spiral.

Fig. 6. System of J.P. Müller, 1854 (from Haeckel, 1862).

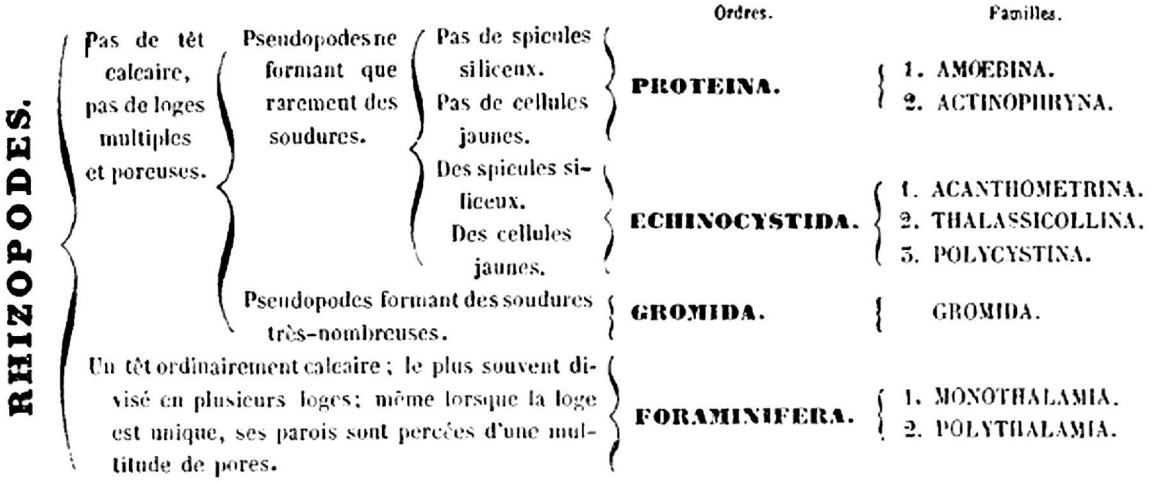


Fig. 7. System of É. Claparède and J. Lachmann, 1858.

main subject of Haeckel was just one of rhizopod groups, he also developed his own system of these organisms (Haeckel, 1862). Following Müller, he divided all rhizopods into those who have a contractile vacuole (Rhizopoda sphygmica) and those who do not have it (Rhizopoda asphycta). He excluded the genus *Actinophrys* from the first group, transferring it, despite the presence of a contractile vacuole, to Rhizopoda asphycta, Acyttaria, Athalamia. Nonetheless, as in Müller's system, this group remained artificial combining naked and testate lobose and filose freshwater amoebae. The second group was divided into Acyttaria and Cytophora based on the absence or presence of the central capsule, respectively. Cytophora included the only Radiolaria group. It was the presence of the central capsule, which Haeckel described, that he considered the defining feature of this group. The taxon Acyttaria, in addition to multi-chambered foraminifera, also included naked representatives and forms with only one chamber.

A. RHIZOPODA SPHYGMICA: Mit contractiler Blase. Pseudopodien niemals Anastomosen bildend, ohne Körnchenströmung.
I. Amoebida. (Gattungen: *Amoeba, Podostoma, Petalopus, Pseudochlamys, Arcella, Echinopyxis, Difflugia, Trinema, Euglypha.*)
B. RHIZOPODA ASPHYCTA: Ohne contractile Blase. Pseudopodien Anastomosen bildend, mit Körnchenströmung.
II. Acyttaria (sive Acyta): Ohne Centralkapsel.
1. Athalamia: Ohne Gehäuse. (Gattungen: *Actinophrys, Trichodiscus, Plagiophrys, Lieberkuehnia.*)
2. Monothalamia: Mit einkammerigem Gehäuse. (Gattungen: *Gromia, Lagynis, Ovulino, Fissurina, Squamulina, Pleurophrys, Cornuspira.*)
3. Polythalamia: Mit vielkammerigem Gehäuse. (Familien: *Acervulinida, Miliolida, Turbinoida, Nautiloida, Alveolinida, Soritida, Nodosarida.*)
III. Cytophora: Mit Centralkapsel: Radiolaria [1]).

Fig. 8. System of E. Haeckel, 1862.

W.B. Carpenter, W.K. Parker and T.R. Jones (Carpenter et al., 1862) wrote a monograph devoted to foraminiferans, but also suggested a classification scheme for all remaining rhizopods. They were probably the first researchers to classify amoeboid protists primarily based on differences in the structure of pseudopodia. They divided the class Rhizopoda into three orders: Lobosa, Radiolaria and Reticulosa.

Carpenter with co-authors drew attention to the extraordinary similarity of the pseudopodia of lobose testate and naked amoebae that, in their opinion, were "...all so closely related as to consistent but one natural order" (Carpenter et al., 1862, p. 16). For this order, which united testate and naked amoebae with broad pseudopodia, they proposed the name Lobosa (from English "lobe", "blade"). Thus, they eliminated the artificial grouping of rhizopods by the presence or absence of a contractile vacuole, and created a taxon, which had existed until recently.

The family Actinophryna, apparently, contained centrohelids, because authors specified that it "... includes certain forms that possess a firm envelope over a larger or smaller portion of their surface..." (Carpenter et al., 1862, p. 15). According to the presence of thin unbranched pseudopodia, this family was included into Müller's taxon Radiolaria. Amoeboid organisms with branched pseudopodia, such as *Gromia* and Foraminifera, were placed in the taxon Reticulosa.

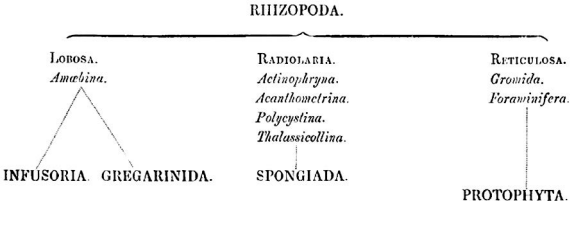


Fig. 9. System of W.B. Carpenter, W.K. Parker and T.R. Jones, 1862.

Four years later after Carpenter and co-authors' publication, E. Haeckel in his monograph "Generelle Morphologie der Organismen" ("General Morphology of Organisms") (1866), revised his views on the rhizopod system and substantially changed it. He subdivided rhizopods into two separate "trunks" ("stamm"). Naked and testate lobose and filose amoebae were removed from Rhizopoda and grouped in a separate "trunk" called Protoplasta. The latter, in turn, was subdivided into two groups, Gymnamoebae (naked amoebae) and Lepamoebae (testate amoeba). The second "trunk", Rhizopoda, contained all the other amoeboid protists. It was divided into three classes: Acyttaria (foraminiferans), Radiolaria and the new class Heliozoa with the only genus *Actinospherium*, while another heliozoan genus *Actinophrys* was placed in the group Monera since Haeckel did not observe its nucleus.

A considerable contribution both to the study of the diversity of rhizopods and to the construction of their system was made by R. Hertwig and E. Lesser (1874) in their monograph "Über Rhizopoden und denselben nahestehende Organismen" ("On rhizopods and related organisms"). They placed all testate freshwater rhizopods in the Monothalamia group, which were divided into Monothalamia Lobosa (having lobose pseudopodia) and Monothalamia Rhizopoda (with thin, root-like pseudopodia). Hertwig and Lesser (1874) divided Haeckel's taxon Heliozoa into two groups: Heliozoa Askeleta, which included actinophryids, the genera *Actinophrys* and *Actinosphaerium*, and Heliozoa Skeletophora. The latter was divided into Chalarothoraca and Desmothoraca. The first group included heliozoans with separate skeletal elements — centrohelids (*Acanthocystis, Raphidiophrys* and *Heterophrys*) and the group Pompholyxophryidae (*Pinacocystis* and *Pompholyxophrys*, as *Hyalolampe*), now belonging to Opisthokonta clade (Galindo et al., 2019). The

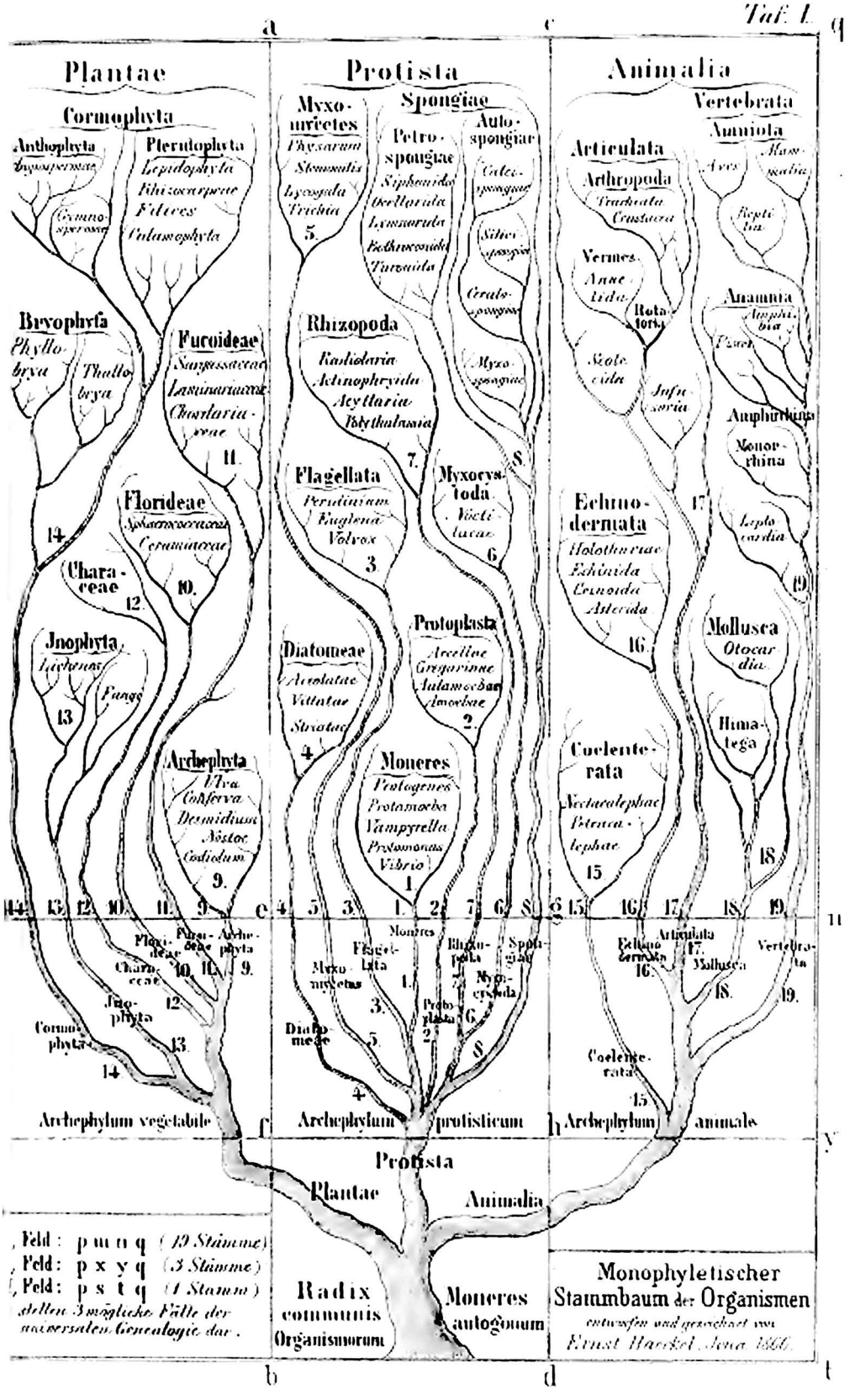


Fig. 10. Phylogenetic tree with "trunks" ("stamm") from E. Haeckel's "Generelle Morphologie der Organismen" (1866).

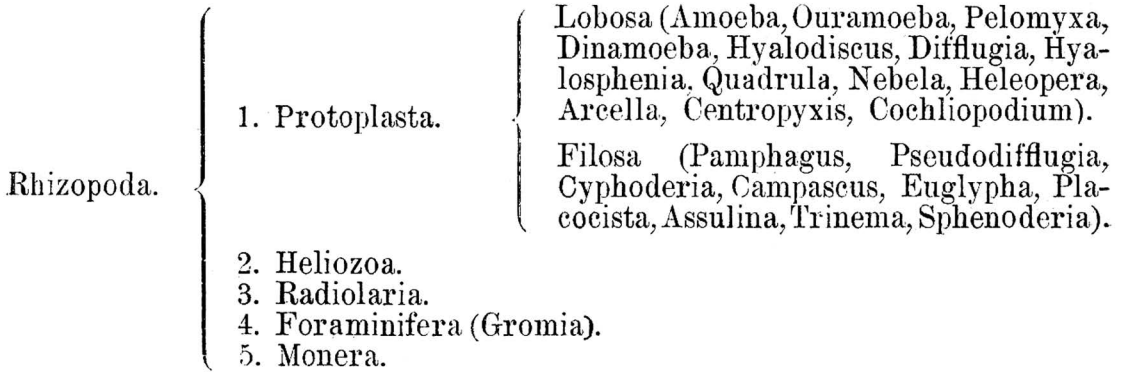


Fig. 11. System of J. Leidy, 1879 (after Averintsev, 1906).

second group included heliozoans with a perforated capsule. It comprised the genus *Clathrulina* described earlier by L.S. Cienkowski (1867) and the new genus *Hedriocystis*. Finally, Hertwig and Lesser (1874) proposed a new name for amoeboid protists as a whole — Sarkodina (from Dujardin's term "sarcode"). This was done, since in fact the root-like pseudopodia are inherent only to their rhizopodial representatives, in particular foraminifera.

In 1877, R. Hertwig (1877) described an unusual amoeboid protist, *Sticholonche zanclea*, living in the marine pelagial and moving with the help of strokes of thin radial pseudopodia. Hertwig noted that the species he described had features of both Heliozoa and Radiolaria, and therefore he did not include it in either taxon. In 1883, H. Fol (1883), also considering *Sticholonche* as an intermediate form between Heliozoa and Radiolaria, created a separate order for this species — Taxopodida.

J. Leidy (1879) in his monograph "Freshwater Rhizopods of North America" described a large number of new species, but also proposed his own classification of rhizopods. The main difference from the classifications of the predecessors was the establishment of the group Filosa, which included testate amoebae with thin, filamentous pseudopodia that did not anastomose. In addition to lobose and filose amoebae, heliozoans, radiolarians, and foraminiferans, Leidy also included in the taxon Rhizopoda an artificial group Monera, which consisted of the smallest organisms, including bacteria.

O. Bütschli (1880–1882) in his three-volume textbook on protozoology removed radiolarians and heliozoans from the Rhizopoda. Rhizopoda, Radiolaria and Heliozoa were listed as three subclasses of the class Sarcodina. He divided the subclass Rhizopoda *per se*, following Schulze, on the basis of the presence or absence of a shell, into the suborders Amoebae and Testacea. Thus, naked lobose (Amoebae lobosa) and reticulose amoeboid protists (Amoebae reticulosa) fell into his taxon Amoebae. Bütschli also subdivided the taxon Testacea into the tribes Imperforata and Perforata. The last group included foraminiferans with "pores" in their shells; the first group included all other testate rhizopods, i.e. lobose and filose testate amoebae, *Gromia* and similar organisms, as well as single- and multi-chambered foraminiferans that did not have "pores" in their shells.

The classification by Y. Delage and E. Hérouard (1896) is of a particular interest because of the inclusion of slime molds (Mycetozoariae) in the Rhizopoda. This was very unusual for works on protists of that time. S. Averintsev wrote: "Then, Delage and Hérouard proposed a rather strange classification of protozoans, where among the rhizopods we find forms that are usually considered as lower fungi, and where forms of Rhizopoda with pseudopodia of various types (for example, *Euglypha* and *Gromia*) are combined into one suborder" (Averintsev, 1906, p. 127).

A. Lang (1901) used the name "Sarcodina" for a taxon corresponding in size to Bütschli's Rhizopoda, and his term "Rhizopoda" referred to rhizopods with reticulose pseudopodia.

G.N. Calkins (1909) established the taxon Actinopoda, in which he combined the radiolarians and heliozoans both having thin, ray-like pseudopodia.

A.A. Schaeffer (1926) was the first to attempt creating a classification of naked lobose amoebae (Carpenter's Lobosa, which appeared in the rank of order in Schaeffer's system), dividing them into five families. Almost all of these families (with the exception of Thecamoebidae) are now

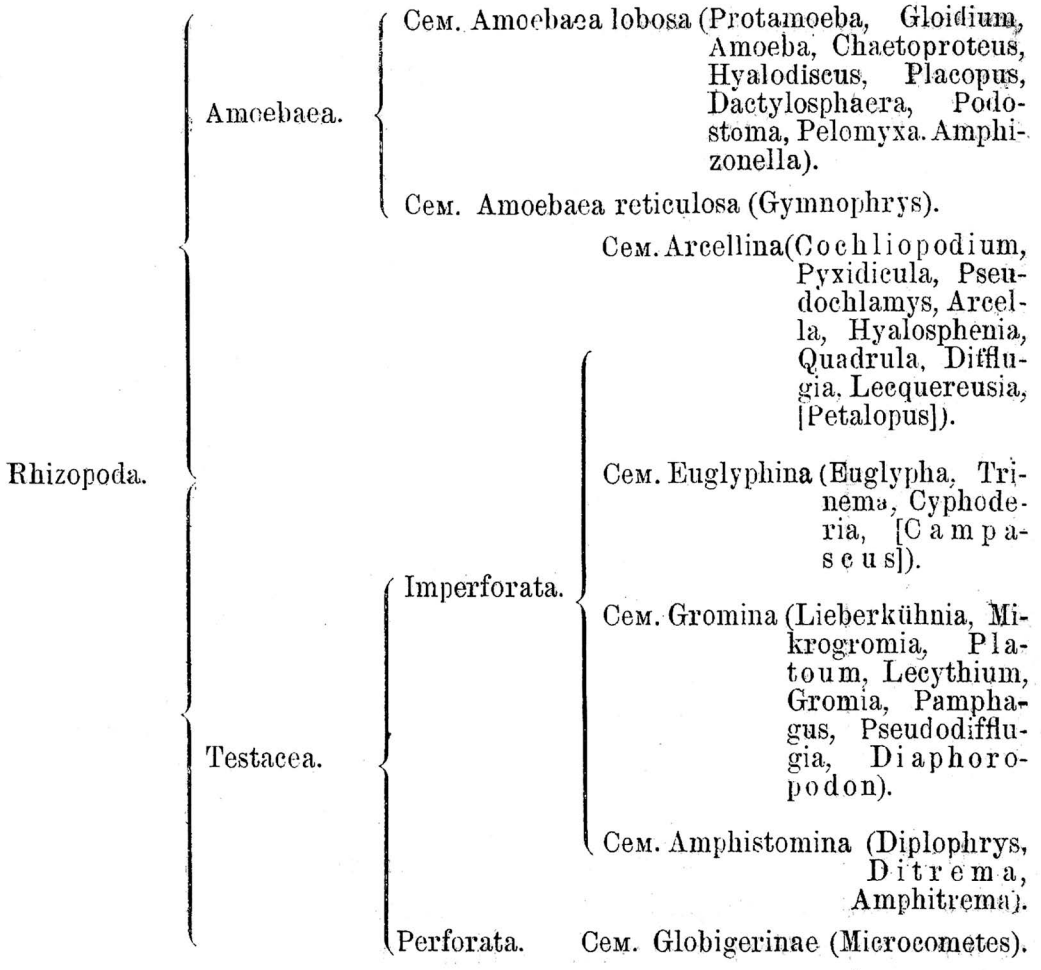


Fig. 12. System of O. Bütschli, 1880–1882 (after Averintsev, 1906).

considered as artificial, and their names now are considered either being invalid or belonging to smaller taxa. At the same time, Schaeffer described many genera of naked lobose amoebae that are still valid nowadays: *Polychaos, Metachaos, Flabellula, Mayorella, Vexillifera* and *Flamella.* Interestingly, the author's observations led him to remove the genus *Cochliopodium* from testate amoebae and include it in naked ones. Schaeffer believed that "...its "shell" is not permanent, but apparently consists of living matter, and seems to be convertible into endoplasm" (Schaeffer, 1926, p. 13). Finally, Schaeffer was the first researcher who consistently applied descriptions of the so-called locomotive forms, describing cells of amoebae during locomotion.

T.L. Jahn and E.C. Bovee (1965) built their classification of rhizopods based on pseudopodia structure and mechanisms of locomotion. They divided all amoeboid protists on Autotractea, organisms with thin filamentous pseudopodia with bidirectional flow of the cytoplasm, and Hydraulia, organisms with tubular pseudopodia or bodies, in which the movement of the more liquid inner component of the cytoplasm occurred due to the contraction of its gel-like part. It was Jahn and Bovee who first noticed the similar structure of pseudopodia in *Amoeba proteus*-like amoebae and of testate lobose amoebae. This led authors to combine these protists into the group Tubulina. Although this idea did not find support among most researchers and the authors themselves subsequently abandoned it, its validity was partly confirmed 40 years later (Smirnov et al., 2005).

In 1964, The Committee on Taxonomy and Taxonomic Problems of the Society of Protozoologists suggested a revised classification of the phylum Protozoa (Honigberg et al., 1964). In their system amoeboid protists were placed in the superclass Sarcodina with three classes, Rhizopodea,

Rhizopodia.

1. Proteomyxiae.
2. Mycetozoariae.
3. Amoebiae.
   - 3a. Gymnamoebida (Amoeba, Protamoeba, Gloidium, Chaetoproteus, Hyalodiscus, Dactylosphaerium, Plakopus, Pelomyxa, Amphyzonella, Podostoma и друг.).
   - 3b. Thecamoebida (Cochliopodium, Arcella, Pseudochlamys, Pyxidicula, Hyalosphenia, Difflugia, Quadrula, Nebela, Heleopera, Lecquereusia, Petalopus, Arcellina).
4. Foraminiferiae.
   - 4a. Imperforata.
     1. Gromidae (Euglypha, Gromia, Hyalopus, Lieberkühnia, Microgromia, Pamphagus, Lecythium, Platoum, Pseudodifflugia, Diaphoropodon, Diplophrys, Ditrema, Amphitrema и др.).
     2. Miliolidae.
     3. Arenacidae.
     4. Globigerinidae(Mikrocometes).
5. Heliozoa.
6. Radiolaria.

Fig. 13. System of Y. Delage and E. Hérouard, 1896 (after Averintsev, 1906).

Actinopodea and also apicomplexans, third class Piroplasmea. The first class included subclasses Lobosia, Filosia, Granuloreticulosia, Mycetozoia and Labyrinthulia. The second class included radiolarians and heliozoans. In this system Mycetozoia contained (as we know now)phylogenetically distant groups, Acrasida, Eumycetozoa and Plasmodiophorida. A new revised classification of the Protozoa was published in 1980 (Levine et al., 1980). In the new system piroplasmids were removed from Rhizopoda, which became a superclass. Rhizopoda included following classes: Lobosea, Acarpomixea, Acrasea, Eumycetozoa, Plasmodiophorea, Filosea, Granuloreticulosea and Xenophyophorea, while superclass Actinopoda included four classes: Acantharea, Polycystinea, Phaeodarea and Heliozoea with Taxopodida as the one of its orders.

Invention of electron microscope

Further development of the classification of rhizopods and protists in general in the second half of the XX century was linked to the emergence

Sarcodina.

I. Lobosa.
   1. Amoebaea (Amoeba, Dactylosphaera).
   2. Testacea (Arcella. Difflugia. Pontigulasia, Lecquereusia, Quadrula, Hyalosphenia).

II. Filosa.
   1. Amphistomina (Diplophrys, Ditrema, Amphitrema).
   2. Monostomina (Microgromia, Platoum, Euglypha. Trinema, Paulinella, Cyphoderia).

III. Rhizopoda.
   1. Nuda (Biomyxa, Gymnophrys и др.).
   2. Foraminifera (10 семействъ; между прочимъ, въ сем. Rhabdamminidae находятся прѣсноводныя: Gromia и Lieberkühnia).

Fig. 14. System of A. Lang, 1901 (after Averintsev, 1906).

Regnum Animalia.
Phylum Protozoa Goldfuss, 1817.
Class Rhizopoda Siebold, 1845.
Order Lobosa Carpenter, 1861.
Suborder Amœbæa Ehrenberg, 1830.
Family Trimastigamœbidæ Pinto, 1922.
Genus Trimastigamœba Whitmore, 1911.
Genus Vahlkampfia Chatton and Lalung Bonnaire, 1912.
Genus Guttulidium Frenzel, 1892.
Family Chaidæ Poche, 1913.
Genus Trichamœba Fromentel, 1874.
Genus Endamœba Leidy, 1879.
Genus Polychaos Schaeffer.
Genus Metachaos Schaeffer.
Genus Chaos Linnæus, 1767.
Genus Pelomyxa Greeff, 1872.
Family Mayorellidæ Schaeffer.
Genus Flabellula Schaeffer.
Genus Mayorella Schaeffer.
Genus Vexillifera Schaeffer.
Genus Striolatus Schaeffer.
Genus Astramœba Vejdovsky, 1881.
Genus Dactylosphærium Hertwig and Lesser, 1874.
Genus Dinamœba Leidy, 1874, emend. Luetken, 1876.
Genus Pontifex Schaeffer.
Family Thecamœbidæ Schaeffer.
Genus Rugipes Schaeffer.
Genus Thecamœba Fromentel, 1874.
Family Hyalodiscidæ Poche, 1913.
Genus Unda Schaeffer.
Genus Hyalodiscus Hertwig and Lesser, 1874.
Genus Gibbodiscus Schaeffer.
Genus Flamella Schaeffer.
Genus Cochliopodium Hertwig and Lesser, 1874.

Fig. 15. System of naked lobose amoebae by A.A. Schaeffer (1926).

and development of the electron microscopy. These studies, for example, allowed revealing different organization of microtubules inside pseudopodia in different groups of heliozoans. Thus, J.A. Kitching (1964) and L.G. Tilney and K.R. Porter (1965) showed that the microtubules of the actinophryid heliozoans *Actinophrys* and *Actinosphaerium* are organized as two nested helices on a cross section. For cent-rohelids, it was shown (Tilney, 1971) that they had another pattern of organization of microtubules in pseudopodia and their "central granule" was actually a microtubule

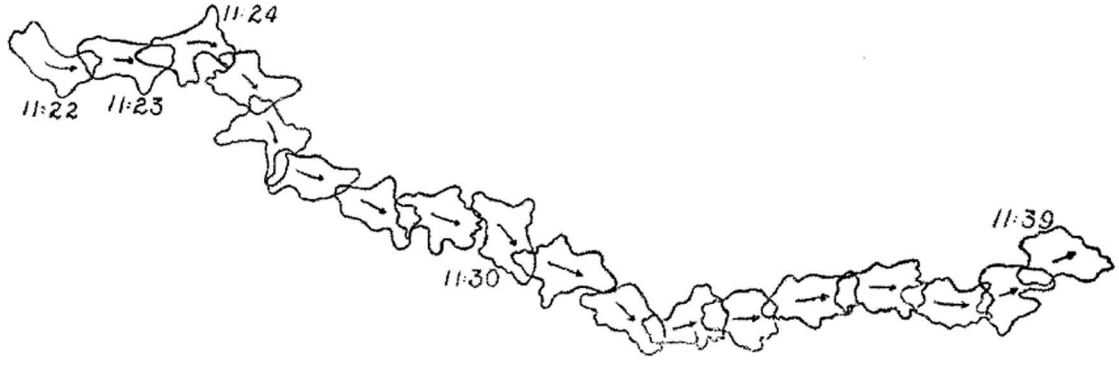


Fig. 16. Line drawings of consequential changes of locomotive form of naked lobose amoeba *Metachaos rarum* (from Schaeffer, 1926).

organizing center (MTOC). Thanks to studies on the fine structure by D.J. Patterson (1985), the genus *Pompholyxophrys* was excluded from centrohelids. Despite the superficial similarity of these two groups, the presence of siliceous scales and the eccentric position of its nucleus, *Pompholyxophrys* was shown to lack microtubules in pseudopodia.

F.C. Page and R.L. Blanton (1985) studied the fine structure of representatives of the orders Schizopyrenida and Acrasida (the latter was previously considered as a part of the Mycetozoa taxon) combining them into a new group Heterolobosea. As autapomorphies for this taxon, the authors listed the presence of an eruptive locomotive form, flagellated, often transitional, stages, discoid mitochondrial cristae, rough endoplasmic reticulum more or less associated with mitochondria, an absence of dictyosomes of the Golgi apparatus and closed intranuclear orthomitosis.

F.C. Page's work (1987) was the pinnacle of the development of a system of naked lobose amoebae based solely on morphological characters. Page also proposed his classification of the Rhizopoda. Page and Blanton (1985) included Heterolobosea as a separate class in the phylum Rhizopoda, with the family Guttulinopsidae as a part of Heterolobosea. Much later (Brown et al., 2012) it was shown that the latter group belongs to the Rhizaria supergroup, which mainly includes rhizo- and filopodial protists. The family Cochliopodiidae was removed from the order Arcellinida (lobose amoebae with an external shell) and separated into an order Himatesmenida as a part of the subclass Testacealobosia of the class Lobosea. The order Pelobiontida was separated as a part of the Caryoblastea. In 2000, A. Rogerson and D.J. Patterson (2000) suggested another system of naked lobose amoebae based solely on morphological characters. It was very similar to Page's, but with the one principle change: authors merged two orders Acanthopodida and Loboreticulatida in one order Centramoebida for amoebae with cytoplasmic MTOCs.

Modern times. Molecular phylogenetics

The first classifications of protists based on the results of the molecular phylogenetic analysis unavoidably suffered from a lack of data. Thus, many of the conclusions were rather hypothetical and speculative.

In one of his works, T. Cavalier-Smith (1993) suggested a classification based on the early analyses of 18S rRNA gene phylogeny. According to it, the taxon Lobosea was polyphyletic. The genus *Pelomyxa* together with the genera *Mastigamoeba, Mastigina*, and *Mastigella* formed the order Mastigamoebida. The genus *Phreatamoeba* was part of a separate order Phreatamoebida. Together, these two orders constituted the class Pelobiontea and belonged to the phylum Archamoebae of the kingdom Archaezoa. At that time, Cavalier-Smith erroneously believed that representatives of these genera ancestrally lacked mitochondria and therefore were the most primitive eukaryotes. As we know today, Archaezoa appeared as a result of the long branch attraction, and the loss of mitochondria was apparently secondary and related either with a parasitic lifestyle or with living in anaerobic habitats. The class Heterolobosea was placed into a separate subkingdom Adictyozoa of the kingdom Protozoa. Lobose amoebae have been assigned to the subkingdom Dictyozoa. Most of them, as classes Lobosea and Filosea, became a part of the phylum Rhizopoda, which was included in the parakingdom Neosarcodina. The family Entamoebidae belonged to the kingdom Entamoebia.

Despite the use of a new kind of data, 18S rRNA gene sequences, the system of rhizopods generally remained very similar to the older, morphology-based one, probably because of the limited number of available sequences. For example, Cavalier-Smith (1993) retained Calkins' taxon Actinopoda uniting heliozoans and radiolarians. He also established the parakingdom Neosarcodina, which included lobose and filose naked and testate amoebae and foraminiferans (a taxon similar in size to Rhizopoda in Bütschli's sense).

In 1998, Cavalier-Smith (1998) used the same marker (18S rRNA gene) and proposed a new classification of eukaryotic organisms. Previously, it was reliably shown (Hinkle et al., 1994; Morin and Mignot, 1996) that Archamoebae actually lost mitochondria secondarily due to the transition to anoxic metabolism. Following these results, Cavalier-Smith (1998) removed Archamoebae from the taxon Archaezoa. Lobose amoebae, Archamoebae (pelobionts and Entamoebidae), and Mycetozoa formed a clade Amoebozoa. Archamoebae together with Mycetozoa formed the group Conosa, which was sister to the taxon Lobosa (lobose amoebae and the flagellate Multicilia). Most of the amoeboid organisms with filose and reticulose pseudopodia (*Euglypha, Gymnophrys, Chlorarachnion*) fall in the new cluster Cercozoa together with flagellates (*Cercomonas, Spongomonas*) and specialized parasites Plasmodiophoridae. Foraminifera represented

Table 1. Summary of classification

Phylum Rhizopoda	Phylum Rhizopoda
Class Heterolobosea	Subclass Testacealobosia
Order Schizopyrenida	Order Himatismenida
Family Vahlkampfiidae	Family Cochliopodiidae
Family Gruberellidae	Order Arcellinida
Order Acrasida	Order Trichosida
Family Acrasidae	Class Caryoblastea
Family Guttulinopsidae	Order Pelobiontida
Class Lobosea	Family Pelomyxidae
Subclass Gymnamoebia	Class Eumycetozoea
Order Euamoebida	Class Plasmodiophorea
Family Amoebidae	Class Filosea
Family Thecamoebidae	Subclass Aconchulinia
Family Hartmannellidae	Order Cristidiscoidida
Family Vannellidae	Family Nucleariidae
Family Paramoebidae	Family Pompholyxophryidae
Family Vexilliferidae	Order Cristivesiculatida
Order Leptomyxida	Family Vampyrellidae
Suborder Rhizoflabellina	Family Arachnulidae
Family Flabellulidae	Subclass Testaceafilosia
Family Leptomyxidae	Class Granuloreticulosea
Suborder Leptoramosina	Order Athalamida
Family Stereomyxidae	Family Biomyxidae
Family Gephyramoebidae	Order Promycetozoida
Order Acanthopodida	Family Reticulomyxidae
Family Acanthamoebidae	Order Monothalamida
Order Loboreticulatida	Order Foraminiferida
Family Corallomyxidae	Class Xenophyophorea
Incertae sedis	
Family Echinamoebidae	
Family Entamoebidae	
Family Hyalodiscidae	

Fig. 17. System of Rhizopoda by F.C. Page (1987).

a separate phylogenetic branch, which was close to Cercozoa. Heterolobose amoebae as a part of the taxon Percolozoa, together with the group Euglenozoa (euglenoids and trypanosomatids), were included in the new infrakingdom Discicristata. Cavalier-Smith (1998) retained Actinopoda as an infrakingdom, although he mentioned that this taxon was "possibly polyphyletic".

Thus, by 1998, the artificial nature of the taxa Rhizopoda and Sarcodina became evident. T. Cavalier-Smith wrote: "Because rRNA sequence has shown that flagellate and amoeboid taxa are phylogenetically intermingled, the names Sarcodina and Rhizopoda are now both abandoned as formal names for taxa. They will however remain useful as non-phylogenetic designations of body form in descriptive and ecological studies, like 'flagellate' or 'alga'; thus 'rhizopod' can continue to be applied in the traditional sense to any amoeba, irrespective of its taxonomic affinity, to contrast it with a flagellate or sporozoan" (Cavalier-Smith, 1998, p. 237–238).

In 2001, L. Amaral Zettler and co-authors (2001) sequenced 18S rRNA gene of several species of naked filose amoebae from the genus *Nuclearia*. Their molecular phylogenetic analysis clearly showed that those amoebae were not related to other filose amoebae from the taxon Cercozoa, but fall into the clade Opisthokonta, which also included Fungi and Animalia.

Cavalier-Smith (2002) established a new infrakingdom Rhizaria, which was subdivided into two phyla — the previously established Cercozoa and the new phylum Retaria, combining Radiolaria (except Phaeodarea) and Foraminifera. Like another taxon of amoeboid protists Amoebozoa, established with the help of molecular phylogenetic analysis, Rhizaria did not have any autapomorphies, except for the molecular signatures. The diagnosis of Rhizaria, in fact, comprised a list of characters of the distinct groups, such as "often with reticulopodia and / or filopodia or axopodia; ancestrally and typically bikont; each centriole ancestrally with a single root of a microtubular band or fan; mitochondrial cristae ancestrally tubular, sometimes secondarily flattened; extrusomes are often kinetocysts" (Cavalier-Smith, 2002, p. 326).

The first molecular phylogeny of centrohelid heliozoans was obtained by T. Cavalier-Smith and E. Chao (2003). According to their results based on the 18S rRNA gene sequences, the group branched with Haptophyta, but without bootstrap support. Same year, Cavalier-Smith (2003) established a taxon Haptista for this clade.

In 2004, S. Polet and co-authors (2004) conducted a phylogenetic analysis based on 18S rRNA sequences. This study showed that Phaeodarea do not branch with other Radiolaria but fall into Cercozoa. Polycystinea and Acantharia formed a clade, which was sister to cercozoans.

S.I. Nikolaev and co-authors (2004), based on the phylogenetic analysis of two markers, 18S rRNA and actin genes, confirmed the monophyly of Rhizaria established by Cavalier-Smith and showed the polyphyly of Heliozoa and Radiolaria. Representatives of Actinophryida formed a single branch within the taxon Heterokonta, which also included pedinellids. The desmotoracid heliozoans *Hedriocystis* and *Clathrulina* found their places inside Cercozoa. At the same time, *Sticholonche zanclea* formed a single branch with Acantharia and Polycystina, thus resolving the issue of the position of this species within radiolarians. Centrohelids, as in the work of Cavalier-Smith and Chao (2003), appeared as a highly supported branch on the phylogenetic tree of eukaryotes, but had an unstable and weakly supported position. In the 18S rRNA gene tree, they branched as a sister group to an unidentified microheliozoan, and together they formed a weakly supported clade with Glaucophyta and Cryptophyta. In the actin tree, Centrohelida, like Cryptophyta and Haptophyta, formed an independent eukaryotic lineage.

Later, F. Burki and co-authors (2009) suggested another root for centrohelids in the phylogenetic tree of eukaryotes. For this, authors sequenced 127 genes using 454 sequencing. As a result, the Centrohelida turned out to be the sister group of the telonemid flagellates. This branch, in turn, was sister to the clade Haptophyta + Cryptophyta. However, the support of this clade still was quite low, less than 70%. In 2015, Cavalier-Smith and coauthors (2015) sequenced a partial transcriptome of tiny centrohelid *Oxnerella micra*, which was included in a 187 genes dataset. This resulted in a monophyletic grouping of centrohelids with haptophytes with moderate support that confirmed taxon Haptista, proposed earlier (Cavalier-Smith, 2003). Finally, Burki et al. (2016) used high-quality transcriptomes (250 genes) of four centrohelid species and broad sampling of eukaryotes. This analysis resulted in unambiguous placing of centrohelids with haptophytes with very high support, thus ultimately closing the question of the phylogenetic position of this group.

In 2004, T. Cavalier-Smith with co-authors presented a new molecular phylogenetic survey devoted to the phylum Amoebozoa only (Cavalier-

Smith et al., 2004). They substantively expanded the taxa set for the analysis based on 18S rRNA gene sequences and established several major clades inside Amoebozoa. In particular, they revealed a new clade comprised naked lobose amoebae with different locomotive morphology (e.g., *Filamoeba, Gephyramoeba* and *Acanthamoeba*) and a flagellate *Phalansterium*, that they called Variosea. Naked lobose amoebae with the flattened locomotive forms (families Vannellidae, Vexilliferidae and Paramoebidae) were grouped in the monophyletic assemblage, named by authors as a class Discosea. This group included either sequenced representatives or groups added on the base of the morphological similarities, namely the order Himatismenida and the new order Dermamoebida with the only family Thecamoebidae in the sense of F.C. Page (1987).

In 2005, S.I. Nikolaev with co-authors resolved another issue related to the taxonomy of amoeboid protists: the position of testate lobose amoebae within Lobosa (Nikolaev et al., 2005). For representatives of two out of three suborders and seven out of thirteen Arcellinida families, a partial sequence of 18S rRNA gene was obtained. Phylogenetic analysis of these sequences showed that Arcellinida is monophyletic and sister to the clade Amoebidae + Hartmannellidae, i.e., is located within the Tubulinea group, lobose amoebae with pseudopodia, tubular in cross section. A complete analysis of the sequences of 18S rRNA gene for two species and a partial analysis of actin gene for one species confirmed the position of the Arcellinida taxon on the phylogenetic tree and its monophyly.

A.V. Smirnov with co-authors continued sequencing 18S rRNA gene of different amoebozoans that leaded to several principal improvements in the naked lobose amoebae system (Smirnov et al., 2005). Firstly, they revealed the clade uniting amoebae with sub-cylindrical pseudopodia including families Amoebidae, Harmannellidae, Leptomyxidae, Echinamoebidae and shelled lobose amoebae. For this clade the name Tubulinea with a rank of a class was applied. For a clade uniting families Paramoebidae, Vexilliferidae and Vannellidae, revealed by T. Cavalier-Smith with co-authors (2004) and named as Glycostylida, a new name Flabellinea was proposed. The clade comprised two families Paramoebidae and Vexilliferidae was designated as the order Dactylopodida and the sister clade containing the family Vannellidae as the order Vannellida. The main feature of this system was a congruence between revealed clades (Tubulinea and Discosea) with the mechanisms of amoeboid movement of their representatives. Tubulineans had pseudopodia tubular, circular, or semicircular in cross-section, at least under certain conditions, and monoaxial cytoplasmic flow in the entire cell (in monopodial naked amoebae) or in every pseudopodium (in polypodial and testate amoebae). In contrast with Tubulinea, discoseans had flattened shapes of the cells and the polyaxial cytoplasmic flow and lack tubular pseudopodia. Thus, these two clades had morphological sinapomorphies. Nonetheless, many genera were left as *incertae sedis*. For example, two genera *Thecamoeba* and *Dermamoeba* branched separately and did not form monophyletic group Dermamoebida that was proposed previously by T. Cavalier-Smith et al. (2004). Members of Variosea also branched separately and were left as *incertae sedis* as well.

In 2011, A.V. Smirnov and T. Cavalier-Smith with co-authors summarized all available data on the molecular phylogeny of naked lobose amoebae and proposed a new system of Amoebozoa (Smirnov et al., 2011). All amoebozoans were divided into two major subphyla Lobosa and Conosa, following Cavalier-Smith (1998). The first subphylum was further subdivided into two classes Tubulinea and Discosea. The principle changes were made mostly in the composition of the second class. Thus, it was subdivided into two subclasses Flabellinea and a new subclass Longamoebia. The first group was expanded and included besides orders Dactylopodida and Vannellida orders Himatismenida, Stygamoebida, Pellitida and Trichosida. The second subclass included order Dermamoebida with genera *Dermamoeba*, *Paradermamoeba* and *Mayorella*, new order Thecamoebida and the order Centramoebida. Subphylum Conosa included Archamoebea and Mycetozoa as in previous classifications, but also the class Variosea.

In 2016, T. Cavalier-Smith and co-authors (2016) conducted a multigene study based on 183 genes and 30 taxa resulted in the establishment of a new class Cutosea. This group unified marine amoebae, that were covered with scales embedded in a common matrix (Kudryavtsev and Pawlowski, 2013; Lahr et al., 2015). According to the tree topology inferred by authors, Cutosea was sister to the clade comprised Tubulinea and Discosea and altogether they constituted the group Lobosa.

Recently (Kang et al., 2017), performed a phylogenomic analysis based on 323 genes and 61 taxa, aimed to resolve major lineages of naked lobose amoebae. These authors showed that Amoebozoa branching on two clades: Tevosa and Discosea. The first branch united Tubulinea and Evosea — a diverse

assemblage combining Cutosea, Archamoebae, Eumycetozoa and Variosea, while the second all amoebae orders with flattened cell body. Thus, these results broke Lobosa (united all naked lobose amoebae except for Variosea) and Conosa (Variosea + Archamoebae + Mycetozoa) concepts.

In another recent phylogenomic study (Brown et al., 2018), the authors analyzed 351 genes and showed that two filose amoebae, *Rigifila* and *Micronuclearia*, found their location in the separate eukaryotic clade called "CRuMs" (from "Collodictyonid + Rigifilida + *Mantamonas*"). Thus, filose amoebae turned out scattered at least between three different eukaryotic lineages: Cercozoa, Opisthokonta and CRuMs.

All recent advances in amoeboid protists' system were summarized in the last revision of higher level classification of eukaryotes by S.M. Adl with co-authors (2019).

Concluding remarks

To summarize, only a few large groups of amoeboid protists, distinguished basing on morphology, have survived until nowadays. Actually, only Foraminifera, established in the first half of the XIX century by d'Orbigny (1926), remained stable. Müller's Radiolaria (Müller, 1858) stayed almost unchanged, except for the removal of Phaeodaria, currently belonging to Cercozoa. All other groups of amoeboid protists that had existed for a long time have lost their taxonomic status. Filosa turned out to be clearly polyphyletic: some of its members fall inside the taxon Cercozoa, while some — inside Opisthokonta, and some other — inside CRuMs. The taxon Rhizopoda in the sense of Bütschli (amoeboid protists except for "Actinopoda", "Heliozoa" + Radiolaria) also was proved clearly polyphyletic. Haeckel's taxon Heliozoa likewise turned out to be polyphyletic. Based on everything written above, the polyphyletic nature of the Sarcodina taxon, which includes Actinopoda (Radiolaria + Heliozoa) and Rhizopoda sensu Bütschli (Lobosa, Filosa, Foraminifera), is also obvious.

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Table 1. Milestones in the study of amoeboid protists.

Year	Author and his contribution to study of amoeboid protists
5th century BC	Herodotus described foraminiferan shells (nummulites) in Egyptian pyramids
1565	C. Gessner described one of the species of Foraminifera
1665	R. Hooke used microscope to observe protists and described a rotaliform foraminiferan
1718	L. Joblot described a heliozoan as "an extraordinary fish"
1755	A.J. Rözel von Rozenhof described a naked amoeba as a "small proteus"
1783	J.C. Eichhorn described heliozoan *Actinosphaerium* as "a star"
1815	M. Leclerc described a testate amoeba *Difflugia*
1826	A. d'Orbigny established an order Foraminifera within the class Cephalopoda
1835	F. Dujardin introduced terms "rhizopodes" and "sarcode" and described *Gromia oviformis*
1838	C.G. Ehrenberg divided amoebae into naked (family Amoebaea) and shelled ones (family Arcellina)
1839	C.G. Ehrenberg proposed a family Polycystina
1841	F. Dujardin published the first system of amoeboid protists divided into three families: Amibiens, Rhizopodes and Actinophryens.
1851	T. Huxley described a radiolarian *Thalassicola*
1854	M. Schulze established an order Testacea for shelled rhizopods
1858	J.P. Müller established Radiolaria
1862	E. Haeckel described central capsule as a defining character of radiolarians
1862	W.B. Carpenter et al. divided Rhizopoda on the base of pseudopodia structure, establishment of an order Lobosa of the class Rhizopoda
1863	H.J. Carter described a centrohelid heliozoan *Acanthocystis*
1866	E. Haeckel established a class Heliozoa as a part of the "stem" Rhizopoda
1867	L.S. Cienkowsky described a desmothoracid heliozoan *Clathrulina elegans*
1874	R. Herwig and E. Lesser suggested a classification of Heliozoa and established Desmothoraca and Sarcodina
1874	R. Greeff described *Pelomyxa palustris*
1877	R. Hertwig described *Sticholonche*
1879	J. Leidy established Filosa, as a suborder of the order Protoplasta
1880–1882	O. Bütschli removed Heliozoa and Radiolaria from Rhizopoda
1883	H. Fol established an order Taxopodida for *Sticholonche*
1909	G.N. Calkins established a class Actinopoda
1926	A.A. Schaeffer suggested a first system of naked lobose amoebae and used a locomotive form as a primary criterion for their classification
1954	K.E. Wohlfarth-Bottermann and F. Krüger described an axoneme with electron microscopy
1965	T.L. Jahn and E.C. Bovee suggested a system of naked lobose amoebae based on pseudopodia structure and united naked and testate amoebae with lobose pseudopodia
1971	L.G. Tilney discovered a MTOC in centrohelid heliozoans
1984	B. Zimmerman et al. united helioflagellates in the order Pedinellales
1985	D.J. Patterson removed *Pompholyxophrys* from centrochelids because of the absence of microtubules in pseudopodia
1985	F.C. Page and R.L. Blanton established a class Heterolobosea

Table 1. (Continuation).

1987	F.C. Page proposed the last morphological system of naked lobose amoebae
1993	T. Cavalier-Smith established a kingdom Archamoebae
1998	T. Cavalier-Smith established a phylum Amoebozoa, a subphylum Conosa, a phylum Cercozoa and grouped heteroloboseans with Euglenozoa
2001	L. Amaral-Zettler et al. placed a filose amoeba *Nuclearia* in Opisthokonta
2002	T. Cavalier-Smith established an infrakingdom Rhizaria and a phylum Retaria
2003	T. Cavalier-Smith and E.Chao conducted the first molecular phylogenetic analysis of centrohelids, which shown weak grouping with haptophytes
2003	T. Cavalier-Smith established an infrakingdom Haptista
2004	S. Polet et al. removed Phaeodaria from Radiolaria and placed it in the phylum Cercozoa
2004	T. Cavalier-Smith et. al. published the first congruent morphological and molecular system of Amoebozoa
2004	S. Nikolaev et al. shown polyphyly of Heliozoa and Radiolaria and included actinophryids in Heterokonta, desmothoracids in Cercozoa and grouped Taxopodida with Acantharia and Polycystina
2005	S. Nikolaev et al. shown that naked and testate lobose amoebae group together inside Tubulinea
2005	A.V. Smirnov et al. proposed the classification of lobose amoebae based on molecular phylogeny. Not yet sequenced taxa were left as *incertae sedis*
2011	A.V. Smirnov and T. Cavalier-Smith jointly proposed a ranked classification of naked lobose amoebae based on morphology and single-gene molecular phylogeny
2016	F. Burki et al. placed centrohelids in Haptista with high support
2017	S. Kang et al. conducted phylogenomic analysis of naked lobose amoebae, shown paraphyly of Lobosa and established Tevosa and Evosea
2018	M. Brown et al. established CRuMs with filose amoebae *Micronuclearia* and *Rigifila* branching inside it.

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