

An Illustrated list of basic morphotypes of Gymnamoebia (Rhizopoda, Lobosea)

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Summary

Detailed analyses of the diversity of locomotive forms among naked lobose amoebae (Lobosea, Gymnamoebia) allow us to construct a typology consisting of 19 “morphotypes” encompassing all known species of the subclass Gymnamoebia. We identify a “morphotype” as a “general pattern of the morphodynamic organisation of the locomotive form of an amoeba”. This system of morphotypes is not a taxonomical one and does not duplicate existing systematic classifications of the respective taxa, although some morphotypes correspond well to the systematic groups of gymnamoebae. Morphotypes are illustrated with schematic drawings and accompanied with brief diagnoses. Selected representatives of different morphotypes are illustrated with photomicrographs. The proposed system of morphotypes seems to be a useful tool for description of gymnamoebae and for elaboration of an iconographic key to gymnamoebae. It can be a helpful tool for preliminary determination of naked amoebae (especially in ecological studies).

Key words: amoebae, Lobosea, Gymnamoebia, morphology, systematic, morphotypes

Introduction

Naked lobose amoebae (phylum Rhizopoda, class Lobosea, subclass Gymnamoebia) are organisms that move by means of so-called amoeboid movement, and do not have constant body form. Since the earliest studies to the present time, this peculiarity is problematic for researchers who need to categorise amoebae (Anderson and Rogerson, 1995; Arndt, 1993; Page, 1991). Bovee (1953) wrote: «One of the knottiest problems in zoology is the specific identification of naked... amebas» (p. 599). This is still an accurate assessment in spite of the fact that new systems of classifying amoeboid organisms have subsequently been developed (see: Bovee, 1970, 1972, 1985; Page, 1987, 1991).

Modern keys to Gymnamoebia (Page, 1983, 1988, 1991) use both light- and electron-microscopical features starting at the levels of families and genera. Actually, even to determine the family or genus, requires nearly a com-

plete set of data needed for correct specific identification (including ultrastructural features). Moreover, the set of criteria needed for a complete and accurate determination of an isolate definitely requires maintenance of clonal cultures (Page, 1988, 1991). The identification of the organism, therefore, more accurately means the identification of a clone. This makes even the preliminary determination of amoebae (up to the family or to the genus) in freshly collected, mixed samples actually impossible, and for these reasons limits the ecological study of amoebae (Arndt, 1993).

The construction of keys to gymnamoebae is a further problem. The traditional attempts to use dichotomous keys (Bovee and Sawyer, 1979; Bovee, 1985; Page, 1983, 1988, 1991) resulted in artificial, unuseful dichotomies and descriptive theses-antitheses pairs, which are very difficult to apply. Actually, a suitable method of organising keys for the gymnamoebae has not been presented, in spite of the wide spread need for a practical key by biologists in a variety of disciplines.

Conception of the «morphotype»

The general consensus is that the locomotive form of the amoeba (its form and cytoplasmic organisation during forward movement) is the most representative characteristic (Schaeffer, 1926; Bovee, 1953; Page, 1976, 1983, 1987, 1988, 1991). Any locomotive form can be characterised by a set of discrete features. These features taken in combination are sufficient to generate a descriptive statement for all known species. Indeed, the number of theoretically possible combinations of features, and their categorisation into types, is immense. Consequently a broad range of locomotive forms can be envisioned. However, only a few of the possible combinations are actually observed in nature. The diversity of locomotive forms among gymnamoebae is broad, but not unlimited. Everyone who has tried to observe amoebae, probably, notes that there is a limited set of locomotive forms. There are characteristic «patterns of organisation» - specific combinations of features that are distinctive locomotive forms characterising each taxon. Every experienced investigator is able to recognise these patterns. This is why one can say that this organism «looks like *Mayorella*» and this one - «like *Chaos*», and the third one is most probably a “rugose thecamoebian”. Experienced investigators usually do not use dichotomous keys, or any other keys at the light-microscopical level of identification. Based on the locomotive form, an experienced observer identifies the genus (or genera) to which the amoeba most likely belongs. This initiates a systematic identification using all necessary techniques. However, in order to work in this very efficient way, it is necessary to first become an “experienced investigator”.

Due to these inherent difficulties, there are “presently less than ten amoebologists in the world today who can expertly recognise the large and middle-size free-living amoebae” (Ishii, 1985, p. 97). Thus, we decided to try to formalise this expert knowledge as a set of typologies that may make it available in a clearer form for a broad range of researchers.

Initially, we surveyed the patterns of organisation of different locomotive forms and found that 19 general patterns include all known free-living species within the subclass Gymnamoebia. We termed these patterns «**morphotypes**», with the following definition: **a morphotype is a general pattern of the morphodynamic organisation of a locomotive form of an amoeba.**

It should be pointed out that one species may belong to more than one morphotype. It is especially likely for the members of the family Amoebidae, many of which are able to adopt two basic forms during locomotion - so called “polytactic” and “orthotactic” (Grebecki and Grebecka, 1978). This is a principal distinction of the proposed system of morphotypes from any taxonomic classification.

Limitations of the present paper

In this paper we established and illustrated 19 morphotypes which, in our opinion, exhaust the diversity of free-living, non-eruptive gymnamoebae - members of the class Lobosea, subclass Gymnamoebia. These morphotypes are illustrated with line drawings and most also with photomicrographs; a brief diagnosis of every morphotype is presented. Among all known gymnamoebae species, we have selected only those that are taxonomically valid (or, in some cases, clearly recognisable) species and listed them according to their morphotype. The list of species is compiled mostly from Page (1976, 1983, 1988, 1991) references for species which were not listed in these monographs are cited in the text.

All the morphotypes are described and illustrated under conditions that the cell is actively moving on the glass or agar surface and is not hindered by the coverslip. These conditions correspond to the standard ones for gymnamoebae observations (see: Page, 1988).

The classification of the morphotypes in its present form does not include the members of the class Heterolobosea. This will be the subject of a special discussion in a forthcoming publication.

List of the morphotypes (Plate 1).

1. **Polytactic** (Figs. 1-3). Polypodial, with several distinctly separated pseudopodia of different size which are formed from the anterior part of the body.

Amoeba proteus, *A. borokensis*, *A. amazonas*, *A. leningradensis*, *Chaos carolinense*, *Ch. illinoisense*, *Ch. nobile*, *Ch. glabrum* (Smirnov and Goodkov, 1997), *Pseudothecamoebea proteoides*, *Deuteramoeba algonquinensis*, *D. mycophaga*.

2. **Orthotactic** (Figs. 4, 5). Orthotactic, body elongated with bell-like cross-section; lateral wrinkles always present.

Amoeba proteus, *A. amazonas*, *A. borokensis*, *Ch. illinoisense*, *Ch. glabrum*.

3. **Palmate** (Fig. 6). Polypodial; with numerous pseudopodia of approximately equal size, which are formed from the basal part of the body; wide fasciculate uroid common.

Polychaos fasciculatum, *P. dubium*, *P. nitidubium*, *P. annulatum* (Smirnov and Goodkov, 1998).

4. **Monotactic** (Figs. 7-13). Monopodial; body subcylindrical with circular cross-section; no lateral wrinkles; never has adhesive uroid.

Trichamoeba sinuosa, *T. myakka*, *T. osseosaccus*, *T. cloaca*, *T. admirata* (Goodkov and Buryakov, 1987, as *Saccamoeba*), *Hydramoeba hydroxena*, *Parachaos zoochlorellae*, *Polychaos annulatum*, *Saccamoeba stagnicola*, *S. limax*, *S. wakulla*, *S. limna*, *S. lucens*, *S.*

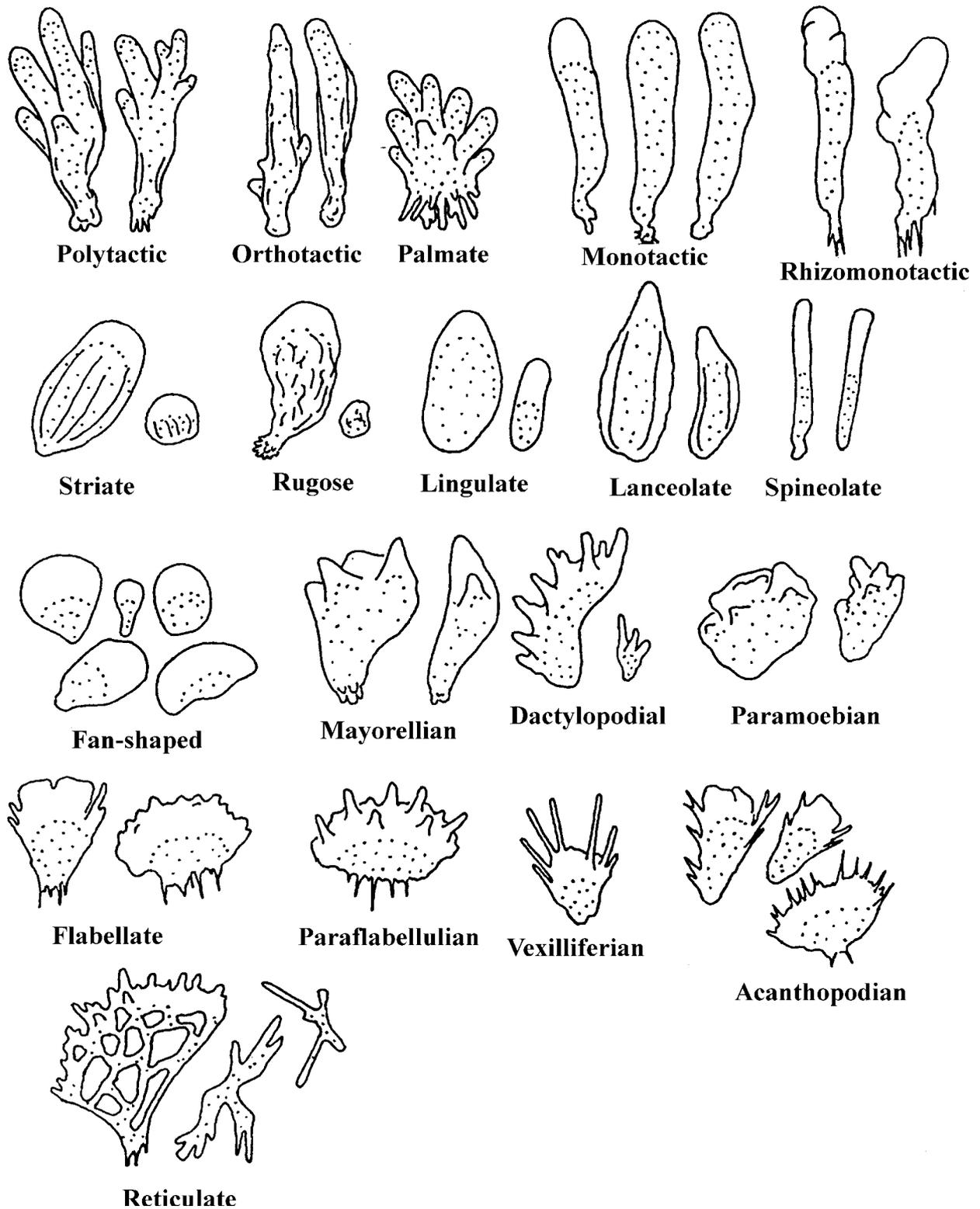


Plate 1. Morphotypes of gymnamoebae. Schematic drawings.

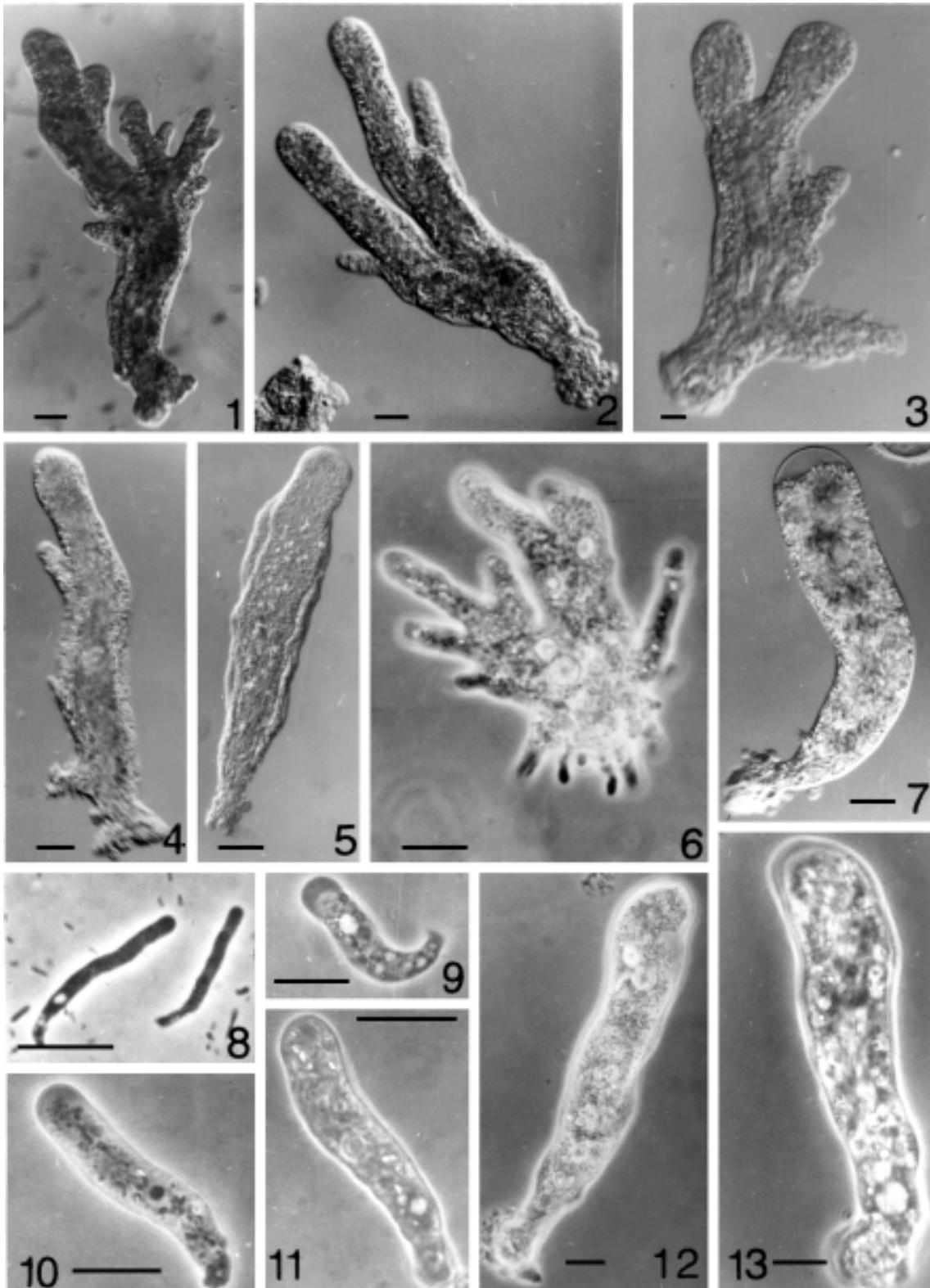


Plate 2. Selected representatives of different morphotypes. **Polytactic:** 1- *Chaos glabrum*, 2, 3 - *Amoeba proteus*. **Orthotactic:** 4 - *Amoeba proteus*, 5 - *Chaos glabrum*. **Palmate:** 6 - *Polychaos annulatum*. **Monotactic:** 7 - *Amoeba proteus*, 8 - *Hartmannella vermiformis*, 9 - *Hartmannella sp.*, 10 - *Saccamoeba stagnicola*, 11 - *S. limax*, 12 - *Polychaos annulatum*, 13 - *Trichamoeba sinuosa*. Scale bar is 25 μ m through.

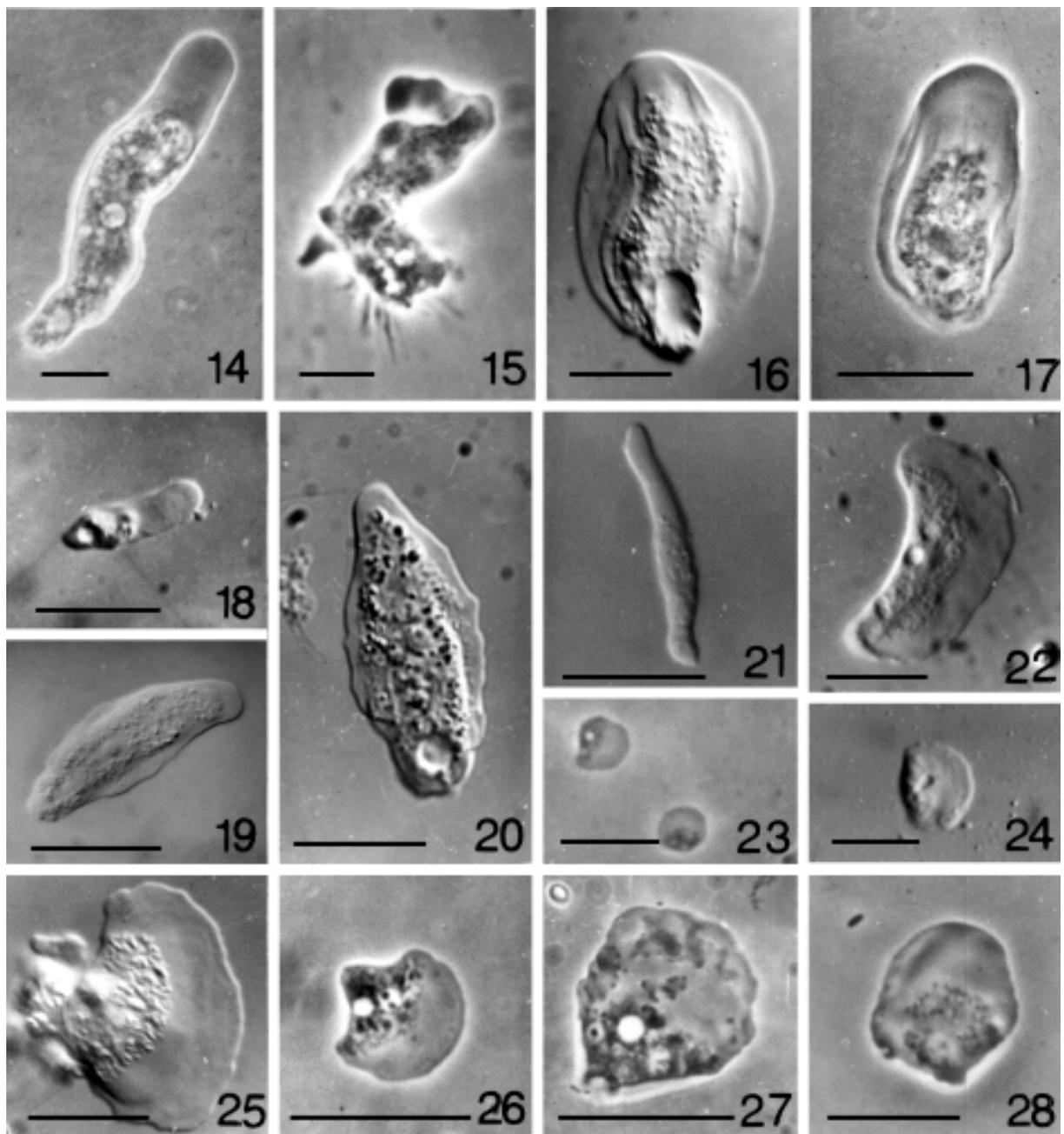


Plate 3. Selected representatives of different morphotypes. **Rhizomonotactic:** 14, 15 - *Rhizamoeba* sp. **Striate:** 16 - *Thecamoeba striata*, 17 - *T. quadrilineata*. **Lingulate:** 18 - *Platyamoeba stenopodia*. **Lanceolate:** 19 - *Paradermamoeba levis*, 20 - *P. valamo*. **Spineolate:** 21 - *Stygamoeba regulata*. **Fan-shaped:** 22 - *Vannella* sp.(1), 23- *Vannella* sp.(2), 24 - *V. platypodia*, 25 - *V. simplex*, 26 - *Vannella* sp.(3), 27 - *Pessonella* sp., 28 - *Platyamoeba plurinucleolus*. Scale bar is 25 mm through.

wellneri (Siemensma, 1987), *S. marina* (Anderson et al., 1997), *Cashia angelica*, *C. limacoides*, *Glaeseria mira*, *Hartmannella cantabrigiensis*, *H. vermiformis*, *H. lobifera* (Smirnov, 1997), *H. abertawensis*, *H. vacuolata* (Anderson et al., 1997), *Nolandella hibernica*, *Amoeba proteus*.

5. **Rhizomonotactic** (Figs. 14, 15). Monopodial; distinct adhesive uroid.

Rhizamoeba polyura, *Rh. saxonica*, *Rh. flabellata*, *Rh. australiensis*, *Rh. schneppii* (Kühn, 1996)

6. **Striate** (Figs. 16, 17). Flattened, ovoid or oblong with regular outline and several nearly parallel dorsal folds.

Thecamoeba striata, *Th. quadrilineata*, *Th. munda*, *Th. orbis*, *Th. hilla*, *Th. sparolata* (Fishbeck and Bovee, 1993, as *Striamoeba*).

7. **Rugose** (not illustrated with photographs, see: Page, 1977). Flattened, ovoid or oblong, with more or less regular outline, dorsal and/or lateral folds and wrinkles which are usually irregular.

Thecamoeba sphaeronucleolus, *Th. verrucosa*, *Th. terricola*, *Th. similis*, *Sappinia diploidea*.

8. **Lingulate** (Fig. 18). Flattened, oblong, with more or less regular outline, without any dorsal and lateral folds and wrinkles.

Dermamoeba granifera, *D. minor*, *Platyamoeba stenopodia*, *Lingulamoeba leei* (Sawyer, 1975a).

9. **Lanceolate** (Figs. 19, 20). Flattened, lancet-like, with distinct lateral flatness, no dorsal folds or wrinkles.

Paradermamoeba valamo (Smirnov and Goodkov, 1993), *P. levis* (Smirnov and Goodkov, 1994)

10. **Spineolate** (Fig. 21). Flattened, thin and very elongate, stick-like, with deep anterior hyaline zone.

Stygamoeba polymorpha (Sawyer, 1975b), *S. regulata* (Smirnov, 1996).

11. **Fan-shaped** (Figs. 22-28). Flattened, semi-circular, fan-shaped or spatulate, with more or less regular outline; distinct separation into very flattened anterior and antero-lateral hyaloplasm and posterior granuloplasmic thickening; anterior edge entire; no subpseudopodia.

Vannella simplex, *V. platypodia*, *V. lata*, *V. cirifera*, *V. miroides*, *V. peregrina* (Smirnov and Fenchel, 1996), *V. devonica*, *V. aberdonica*, *V. caledonica*, *V. arabica*, *V. anglica*, *V. septentrionalis*, *V. sensilis*, *Pessonella marginata*, *Platyamoeba placida*, *P. plurinucleolus*, *P. calycinucleolus*, *P. bursella*, *P. australis*, *P. mainensis*, *P. flabellata*, *P. murchelanoi* (Sawyer, 1975b), *P. langae* (Sawyer, 1975b), *P. weinsteini* (Sawyer, 1975b), *P. douvresi* (Sawyer, 1975b), *Clydonella rosenfeldi* (Sawyer, 1975b), *C. sindermani* (Sawyer, 1975b), *C. wardi* (Sawyer, 1975b).

12. **Mayorellian** (Figs. 29-31). Flattened, irregularly triangular or oblong, anterior hyaline border with a few blunt, conical, hyaline sub-pseudopodia of similar lengths.

Mayorella viridis, *M. cantabrigiensis*, *M. vespertilioides*, *M. penardi*, *M. bigemma*, *M. pussardi*, *M.*

kuwaitensis, *M. gemmifera*, *M. dactylifera* (Goodkov and Buryakov, 1988).

13. **Dactylopodial** (Figs. 32-34). Flattened, irregularly triangular or of variable shape, wide anterior hyaline zone with distinct frontal or fronto-lateral hyaline dactylopodia.

Paramoeba eilhardi, *Pseudoparamoeba pagei*, *Korotnevella bulla*, *K. stella*, *K. nivo* (Smirnov, 1997b).

14. **Flabellate** (Figs. 35, 36). Flattened, irregularly flabellate, average length/breadth ratio near 1.0, prominent anterior hyaloplasm with uneven frontal edge, no subpseudopodia from hyaline zone, though that zone may become cleft, trailing adhesive uroidal filaments.

Flabellula citata, *F. calkinsi*, *F. demetica*, *F. trinovantica*, *F. baltica* (Smirnov, 1999).

15. **Paraflabellulian** (Figs. 37, 38). Flattened, irregularly flabellate, average length/breadth ratio near 1.0, prominent anterior hyaloplasm with very short narrow subpseudopodia produced from hyaline zone, trailing adhesive uroidal filaments.

Paraflabellula reniformis, *P. hoguae* (Sawyer, 1975a, as *Flabellula*), *Flamella citrensis*, *Flamella tiara* (Fishbeck and Bovee, 1993).

16. **Paramoebian** (not illustrated with photographs, see: Page, 1983). Flattened, irregularly fan-shaped, length/breadth ratio more than 1.0, flattened anterior hyaloplasmic lobe with irregular edge, a few very short, blunt projections from hyaloplasm zone and longitudinal dorsal ridges are common, no adhesive uroid.

Neoparamoeba aestuarina, *N. pemaquidensis*.

17. **Vexilliferian** (Figs. 39, 40). Flattened, rather irregularly triangular, not numerous short and long slender, tapering or linear subpseudopodia produced from anterior hyaline zone.

Vexillifera bacillipedes, *V. granatensis*, *V. minutissima*, *V. armata*, *V. telmathalassa*.

18. **Acanthopodian** (Figs. 41, 42). Rather flattened, somewhat irregular in outline, numerous short, slender, flexible, tapering subpseudopodia, sometimes furcate near their base, which are produced from a broad, hyaline lobopodium.

All members of the genera *Acanthamoeba*, *Protacanthamoeba*, *Echinamoeba*, *Filamoeba*, *Comandonia*.

19. **Reticulate** (not illustrated with photographs, see: Page, 1983, 1988). Flattened and expanded, reticulate, with loboreticulopodia.

Gephyramoeba delicatula, *Leptomyxa reticulata*, *Stereomyxa ramosa*, *S. angulosa*, *Corallomyxa chattoni*, *C. mutabilis*.

Concluding remarks

Even Penard (1902) termed amoebae as “striate”, “verrucose”, etc.; so, formally, he used some morphotypes

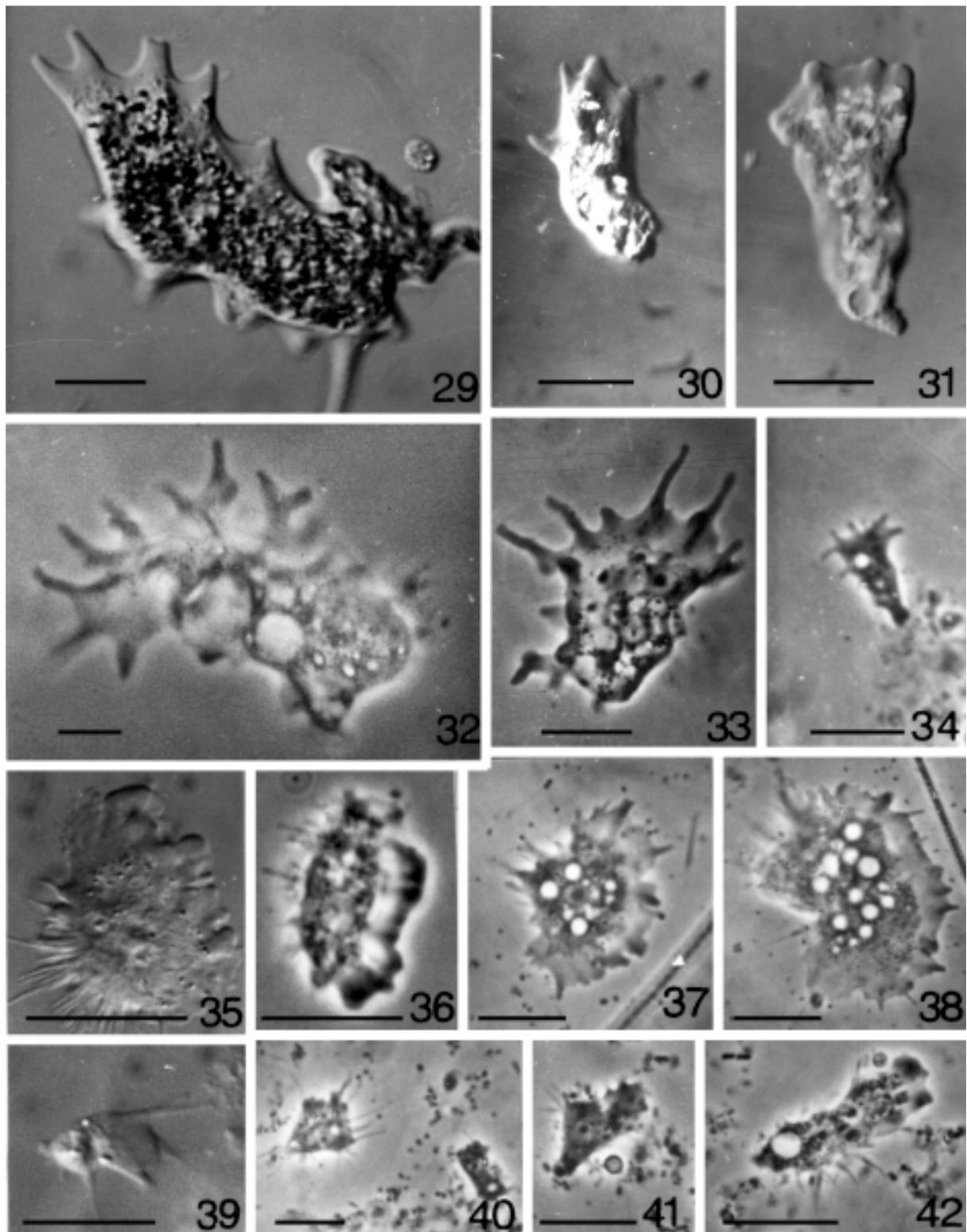


Plate 4. Selected representatives of different morphotypes. **Mayorellian:** 29 - *Mayorella cantabrigiensis*, 30-31 - *M. vespertilioides*. **Dactylopodial:** 32 - *Korotnevella bulla*, 33 - *K. stella*, 34 - *Korotnevella* sp. **Flabellate:** 35, 36 - *Flabellula baltica*. **Paraflabellulian:** 37, 38 - *Flamella* sp. **Vexilliferian:** 39 - *Vexillifera bacillipedes*, 40 - *Vexillifera* sp. **Acanthopodial:** 41, 42 - *Acanthamoeba* spp. Scale bar is 25 μ m through.

in his descriptions. As mentioned above, some widely used terms and trivial names (proteus-like amoeba, limax amoeba, etc.) practically mean morphotypes, but only a few of them were more or less clearly defined (Page, 1974, 1976). Bovee (1953) classified so-called life forms of amoebae. He illustrated 20 species in all possible life forms - non-moving, indirectly moving, locomotive, floating, and his system is an excellent vertical analysis of amoeba diversity. However, he did not try to make a horizontal analysis - i.e. to classify comparable life forms of different species. Later an attempt to image and classify the diversity of locomotive forms of amoebae was made by Ishii (1985), but this attempt was also incomplete because this classification was not based on a more or less strong theoretical basis. Recently Anderson and Rogerson (1995) proposed a system of four most common morphotypes of naked amoebae for use in ecological studies that can include all known species, but it is not intended to be a fine-grained analysis of locomotive forms as presented here. They actually came most close to the classification which is described here, however, to exhaust the diversity of the locomotive forms of amoebae was not the aim of their classification.

The remarkable feature of our system is that all known gymnamoebae species (we tested more than 200 species) were recognised as belonging to the proposed morphotypes without serious doubts. This supports the idea that morphotypes could be a useful and easily applied method for gymnamoebae definition and description. The system of morphotypes seems to be a very productive basis for elaboration of an iconographic key to gymnamoebae, especially as a guide to categorisation of the higher level taxa (families and genera).

The conception of the morphotypes was initiated based on an application of the regional atlases of gymnamoebae species, which is exemplified in a forthcoming publication (Smirnov, 1999). The morphotypes could be an excellent tool for systematisation and organisation of the atlas of species. The employment of this new system unifies the description of amoebae based on locomotive form, and makes it much easier to identify major groups of amoebae, because the «morphotype» represents a combination of many features, parsimoniously categorised by a single label. This approach facilitates identifying amoebae based on the total set of attributes in combination «as a whole» rather than using a collection of seemingly disparate indicators as has been the approach heretofore.

The system of morphotypes is not a taxonomic classification, although some morphotypes correspond well to the systematic groups (i.e. acanthamoebian and vexilliferian morphotypes). However, in some cases it makes the existing shortcomings of the systematics clearly apparent. A very remarkable example is that the proposed system makes evident the close similarity of *Pseudothecamoeba* (traditionally placed in the family

Thecamoebidae) with the members of the family Amoebidae, and this fact was already noted on the basis of other features by Page (1988). Another example is that all the members of the family Vannellidae belong to one of our proposed morphotypes, with one exception - *Platyamoeba stenopodia*. This species appeared to be more similar to the smooth thecamoebians, and this fact also was already noted by Page and Blakey (1979).

During field and laboratory studies, even the determination of the morphotype (for example, in ecological studies) gives additional information about the possible systematic position of an amoeba (it outlines the list of species, to which an isolate could belong). Moreover, it is much more correct than a preliminary determination up to the family or genus level by use of existing keys. There is no need for clonal cultures and detailed microscopic analyses as required for most taxonomic keys. However, we do not consider the present paper as a tool for ecologists - this topic will be the subject of a special publication. Within the system of morphotypes, one species could belong to more than one morphotype - depending on its locomotive state at different times. This reflects once more the dynamic property of amoeboid cell organisation. However to resolve this possible confusion taxonomically requires the elaboration of a special iconographic key which associates every observed morphotype with a taxonomic species. This key (in electronic form) is currently in preparation. It must be acknowledged that application of the proposed list of morphotypes for assessing amoeba diversity may result in enumerating more morphotypes than the actual number of species in the sample, since at present there is not a simple rule for making a one to one correspondence between morphotype and species. However, it is not in contradiction with the proposed conception of a morphotype which is a categorisation more inclusive than the species level - within its framework a morphotype may be either equal to a species (when the species belongs to only one morphotype) or not equivalent to a species (for those cases where the species may belong to two or more morphotypes).

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