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ORIGINAL PAPER

A New Classification of the Dictyostelids

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Traditional morphology-based taxonomy of dictyostelids is rejected by molecular phylogeny. A new classification is presented based on monophyletic entities with consistent and strong molecular phylogenetic support and that are, as far as possible, morphologically recognizable. All newly named clades are diagnosed with small subunit ribosomal RNA (18S rRNA) sequence signatures plus morphological synapomorphies where possible. The two major molecular clades are given the rank of order, as Acytosteliales ord. nov. and Dictyosteliales. The two major clades within each of these orders are recognized and given the rank of family as, respectively, Acytosteliaceae and Cavenderiaceae fam. nov. in Acytosteliales, and Dictyosteliaceae and Raperosteliaceae fam. nov. in Dictyosteliales. Twelve genera are recognized: *Cavenderia* gen. nov. in Cavenderiaceae, *Acytostelium*, *Rostrostelium* gen. nov. and *Heterostelium* gen. nov. in Acytosteliaceae, *Tieghemostelium* gen. nov., *Hagiwaraea* gen. nov., *Raperostelium* gen. nov. and *Speleostelium* gen. nov. in Raperosteliaceae, and *Dictyostelium* and *Polysphondylium* in Dictyosteliaceae. The "*polycephalum*" complex is treated as *Coremiostelium* gen. nov. (not assigned to family) and the "*polycarpum*" complex as *Synstelium* gen. nov. (not assigned to order and family). *Coenonia*, which may not be a dictyostelid, is treated as a genus incertae sedis. Eighty-eight new combinations are made at species and variety level, and *Dictyostelium ammophilum* is validated.

Key words: Classification; dictyostelids; molecular characters; nomenclature; phylogeny; taxonomy.

Introduction

Dictyostelids are heterotrophic amoebae, also known informally as cellular slime molds or social amoebae. They are commonly isolated from a variety of soils worldwide and are ecologically important as predators of soil bacteria. Dictyostelids are particularly well known and widely studied because of their lifestyle, which alternates regularly between unicellular and multicellular (sorocarpic) stages. This "aggregative multicellular" behaviour has also led to their widespread use as molecular and evolutionary models, beginning largely with *Dictyostelium discoideum* but now including a handful of taxa from across the phylogeny (Singh et al. 2015). The identification and taxonomy of dictyostelids has traditionally been

based on the morphology of their sorocarps and related characters, as their amoebae appear to be indistinguishable. While new species continue to be identified based on morphological characters (e.g. Cavender et al. 2016), molecular phylogeny indicates that much of the traditional taxonomy is fundamentally flawed, particularly at the deepest taxonomic levels. Therefore, major taxonomic revision has been needed for some time.

The first dictyostelid was isolated and described by Oskar Brefeld as *Dictyostelium mucoroides* (Brefeld 1869), the genus name from the Greek "dictyon" (net) and "stele" (column) referring to the net-like appearance of the cells in the stalks of the fructifications (sorocarps). By the end of the 19th century three further species of *Dictyostelium* had been described, *D. lacteum* and *D. roseum* by van Tieghem (1880), and *D. sphaerocephalum* by Saccardo and Marchal (Marchal 1885), the latter based on *Hyalostilbum sphaerocephalum* (Oudemans 1885). Two new genera were also added, *Coenonia* with the single species *C. denticulata* (van Tieghem 1884) and *Polysphondylium* with the single species *P. violaceum* (Brefeld 1884). *Coenonia* was characterized, in part, by the crampon-shaped base of the stalks and by the cupule-like structure containing the spores, whereas *Polysphondylium* was characterized, above all, by whorls of regularly spaced side branches on the main axial stalk of the sorocarp. In 1900 dictyostelids were known from Europe only, but since then well over a hundred species of *Dictyostelium* and more than 30 species of *Polysphondylium* have been described from all over the world (see Raper 1984 for an excellent summary of the period up to then). In addition, one further genus was added, *Acytostelium* (Raper 1956), characterized mainly by the acellular stalks of the sorocarps. This differs from all other dictyostelids, in which a substantial portion of the aggregate is sacrificed to form a stalk composed of dead cells. *Acytostelium* has 16 described species to date, and new species of *Dictyostelium, Polysphondylium* and *Acytostelium* are being added continuously. However, the enigmatic *Coenonia denticulata* was lost and never recollected (Raper 1984) and the genus remains monospecific, with no available material.

During the last 15 years, increasingly refined cladistic analyses (Swanson et al. 2002) together with molecular phylogenetics (Romeralo et al. 2007, 2011; Schaap et al. 2006; Sheikh et al. 2014; Singh et al. 2016) have shown that the traditional, morphology-based taxonomy of the dictyostelids does not reflect phylogenetic relationships. Instead of three genera, eight distinct molecular clades have been consistently and robustly identified based primarily on well-resolved small subunit ribosomal RNA (SSU rRNA) trees (Romeralo et al. 2011; Schaap et al. 2006). Where tested, these relationships have also been confirmed by

cladistics analysis of morphological characters (Swanson et al. 2002) and/or molecular phylogeny based on alpha-tubulin (atub) and atub + SSU rRNA (Schaap et al. 2006), internally transcribed spacer (ITS) + 5.8S rRNA (Romeralo et al. 2007), ITS + SSU rRNA (Romeralo et al. 2011), and multi-protein phylogeny (Romeralo et al. 2013; Sheikh et al. 2015; Singh et al. 2016).

Most importantly, none of the eight main molecular clades correspond to traditional genera. Until now, these clades have been informally denoted as Groups 1, 2A, 2B, 3, and 4, plus complexes "*polycarpum*", "*polycephalum*", and "*violaceum*", with the three traditional morphotypes distributed across them. Thus, traditional species of *Dictyostelium* (dictyostelid morphotypes) are found in Groups 1, 2B, 3 and 4, and in the "*polycarpum*", "*polycephalum*", and "*violaceum*" complexes, while traditional species of *Polysphondylium* (polysphondylid morphotypes) are found in Group 2B and the "*violaceum*" complex, and species of *Acytostelium* (acytostelid morphotypes) in Groups 2A and 2B (Romeralo et al. 2007; Schaap et al. 2006) or even deeper in the tree (Singh et al. 2016).

Our aim here is to present, on the basis of existing nomenclature, a new classification of the dictyostelids at the levels of order, family and genus. With the exception of the root, the taxonomy is based on monophyletic entities that are strongly and consistently reproduced by small subunit ribosomal RNA (SSU rRNA) phylogenies and not contradicted by any other molecular data (Supplementary Material Fig. S1; Romeralo et al. 2011; Schaap et al. 2006). SSU rRNA phylogeny is essential for this as it is the only data available for the vast majority of dictyostelid species. However, all major groups have been confirmed where tested by other molecular data, specifically SSU ITS + 5.8S (Romeralo et al. 2007), and atub and atub+SSU rRNA (Schaap et al. 2006), and mitochondrial genes (Heidel et al. 2008). The taxa proposed here are, as far as possible, also morphologically recognizable. The position of the root of the dictyostelid tree (between Groups 1+2 and 3+4), while not well resolved by SSU rRNA (Schaap et al. 2006), is strongly and consistently supported by three distinct multi-protein studies (Romeralo et al. 2011; Sheikh et al. 2014; Singh et al. 2016).

Given the dearth of morphological synapormorphies for many dictyostelid groups, all new taxa are also diagnosed with sequence signatures based on SSU rRNA, the most widely used taxonomic molecular marker for eukaryotes and the only marker available for most dictyostelids. The approach here is conservative, and there is considerable potential for further taxonomic subdivision. Taxonomic problems at species level, such as the many

instances of morphologically similar but phylogenetically distinct taxa (cryptic species) scattered throughout the dictyostelid tree (Mehdaibadi et al. 2009; Romeralo et al. 2011), are not dealt with here. However, the new classification is also meant to be a framework for future work at the species level.

Results

We propose that the two major clades in the phylogeny of the dictyostelids (Fig. 1) are given the rank of order, as Acytosteliales ord. nov. (molecular groups 1, 2A and 2B) and Dictyosteliales (molecular groups 3, 4 and molecular complexes "*polycephalum*" and "*violaceum*"). We further propose that the two major clades within each order are given the rank of family, as Acytosteliaceae and Cavenderiaceae fam. nov. in Acytosteliales and Dictyosteliaceae and Raperosteliaceae fam. nov. in Dictyosteliales (Fig. 1). The "*polycephalum*" complex, with a still contentious position within Dictyosteliales, is not assigned to family, and the "*polycarpum*" complex, with a still contentious position in the entire phylogeny, is not assigned to either order or family.

Twelve taxa are recognized at the genus level (Fig. 1), *Cavenderia* gen. nov. corresponding to Group 1, *Acytostelium* corresponding to Group 2A, *Rostrostelium* gen. nov. currently including only *Acytostelium ellipticum* in Group 2B, *Heterostelium* gen. nov. corresponding to the remainder of Group 2B excluding *Acytostelium ellipticum*, *Speleostelium* gen. nov. currently including only *Dictyostelium caveatum*, *Tieghemostelium* gen. nov. corresponding to Group 3A, *Hagiwaraea* gen. nov. corresponding to Group 3B, *Raperostelium* gen. nov. corresponding to Group 3C, *Dictyostelium* corresponding to Group 4, *Coremiostelium* gen. nov. corresponding to the "*polycephalum*" complex, *Polysphondylium* corresponding to the "*violaceum*" complex, and *Synstelium* gen. nov. corresponding to the "*polycarpum*" complex. The enigmatic *Coenonia* is treated as a genus incertae sedis.

Taxonomy

Acytosteliales S.Baldauf, S.Sheikh & Thulin, ord. nov. (Index Fungorum ID IF553650). **Type:** *Acytostelium* Raper

Diagnosis: New order comprising the two families Acytosteliaceae and Cavenderiaceae, which differs from Dictyosteliales and the unplaced genus *Synstelium* together by having in the SSU rRNA gene C (not T) in the nucleotide position 539 and CTC (not CTA) in the positions 1448-1450 of Supplementary Material alignment S2 (Figs 2, 3A).

Description: Sorocarps with cellular or acellular stalks, colorless, white-hyaline or pale yellow, solitary or loosely to tightly clustered, branching rare and usually sparse or irregular where it occurs, sometimes with regularly spaced branches, the sorogens sometimes ventricose-rostrate. Spores globose to irregularly rounded or ellipsoid, sometimes oblong or reniform in outline, granules present or absent. Microcysts and macrocysts sometimes present. Streaming aggregation, slug migration rare, sometimes stalked, acrasin glorin or mostly unknown.

Acytosteliaceae Raper ex Raper & Quinlan, J. Gen. Microbiol. 18: 18 (1958). **Type:** *Acytostelium* Raper

Family comprising three genera, *Acytostelium, Rostrostelium* and *Heterostelium*.

Description: Sorocarps with cellular or acellular stalks, colorless or white hyaline, solitary or loosely to tightly clustered, branching rare and usually sparse where it occurs, sometimes with regularly spaced branches, the sorogens sometimes ventricose-rostrate. Spores globose to irregularly rounded or ellipsoid, granules present or absent. Microcysts and macrocysts sometimes present. Streaming aggregation, slug migration rare, sometimes stalked, acrasin glorin or mostly unknown.

Acytostelium Raper, Mycologia 48: 179 (1956). **Type:** *Acytostelium leptosomum* Raper (Fig. 4)

Description: Sorocarps with acellular stalks, colorless, solitary to loosely clustered (gregarious), slender and delicate, 0.2-3.0 mm in height, branching rare and sparse where it occurs. Spores globose, subglobose or irregularly rounded, 4.0-8.5 µm in diameter, granules rare or inconspicuous. Microcysts known, macrocysts unknown. Streaming aggregation, slug migration rare, acrasin unknown.

Acytostelium aggregatum Cavender & Vadell, Mycologia 92: 1004 (2000)

Acytostelium amazonicum Cavender & Vadell, Mycologia 92: 995 (2000)

Acytostelium anastomosans Cavender et al., Mycologia 97: 497 (2005)

Acytostelium digitatum Cavender & Vadell, Mycologia 92: 997 (2000)

Acytostelium irregularosporum H.Hagiw., Bull. Natl. Sci. Mus., Tokyo 14: 364 (1971)

Acytostelium leptosomum Raper, Mycologia 48: 179 (1956)

Acytostelium longisorophorum Cavender et al., Mycologia 97: 498 (2005)

Acytostelium magniphorum Cavender & Vadell, Mycologia 92: 1000 (2000)

Acytostelium magnisorum Cavender et al., Mycologia 97: 499 (2005)

Acytostelium minutissimum Cavender & Vadell, Mycologia 92: 1002 (2000)

Acytostelium pendulum Cavender & Vadell, Mycologia 92: 1001 (2000)

Acytostelium reticulatum Cavender & Vadell, Mycologia 92: 998 (2000)

Acytostelium serpentarium Cavender et al., Mycologia 97: 500 (2005)

Acytostelium singulare Cavender et al., Mycologia 97: 501 (2005)

Acytostelium subglobosum Cavender, Amer. J. Bot. 63: 61 (1976)

Rostrostelium S.Baldauf, S.Sheikh & Thulin, gen. nov. (Index Fungorum IF553651). **Type:** *Rostrostelium ellipticum* (Cavender) S.Baldauf, S.Sheikh & Thulin (Fig. 5)

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Diagnosis: New genus similar to *Acytostelium* in having sorocarps with a simple acellular stalk, but differing from all species of this genus by its ellipsoid (not globose, subglobose or irregularly rounded) spores. Differs from *Heterostelium* by having sorocarps with an acellular stalk and from both *Acytostelium* and *Heterostelium* by having ventricose-rostrate sorogens and by having in the SSU rRNA gene ATGG (not CAAG, CAGA, AAGA, TAGA) in the nucleotide positions 133-136 and TAATTA (not CAATTT, AAATTG, CAATTG) in positions 540-545 of Supplementary Material alignment S3 (Figs 2, 3B).

Description: Sorocarps with acellular stalks, solitary or gregarious, delicate, unbranched, 0.2-1.0 mm in height, colorless, the sorogens ventricose-rostrate. Spores ellipsoid, 5.0-6.0 × 2.5-3.0 µm, polar granules rare. Microcysts known, macrocysts unknown. Streaming aggregation, slug migration stalked, acrasin unknown.

Etymology: "Rostro-" in the name alludes to the characteristically rostrate (beaked) sorogens of this genus.

Rostrostelium ellipticum (Cavender) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553652). *Acytostelium ellipticum* Cavender, J. Gen. Microbiol. 62: 119 (1970)

Heterostelium S.Baldauf, S.Sheikh & Thulin, gen. nov. (Index Fungorum IF553653). **Type:** *Heterostelium pallidum* (Olive) S.Baldauf, S.Sheikh & Thulin (Fig. 6)

Diagnosis: New genus related to *Acytostelium and Rostrostelium*, from both of which it differs by having sorocarps with a cellular stalk and by having in the SSU rRNA gene AGG (not CGG) in the nucleotide positions 364-366 and GGG (not GAG) in the positions 535-537 of Supplementary Material alignment S4 (Fig. 2, 3C).

Description: Sorocarps with cellular stalks, white-hyaline, solitary or loosely to tightly clustered, unbranched or sparsely branched or with whorls of regularly spaced branches, small and often delicate, mostly <10 mm in height (range 0.2-15 mm). Spores highly variable, granules present/absent consolidated/unconsolidated, generally 3.5-8.0 × 2.0-4.0 μm (rarely up to 11.5 × 5.8 μm). Microcysts commonly observed, sometimes also macrocysts. Streaming aggregation, often of violaceum type (fragmenting to form separate sorocarps), slug migration stalked when present, acrasin glorin (*H. pallidum*) or unknown.

Etymology: The prefix "hetero-" in the name alludes to the great variation in sorocarp morphology within this genus.

Heterostelium album (Olive) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553654). *Polysphondylium album* Olive, Proc. Amer. Acad. Arts 37: 342 (1901)

Heterostelium ampliverticillatum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553663). *Polysphondylium ampliverticillatum* Cavender et al., Mycologia 108: 85 (2016)

Heterostelium anisocaule (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553664). *Polysphondylium anisocaule* Cavender et al., New Zealand J. Bot. 40: 240 (2002)

Heterostelium arachnoideum (Vadell & Cavender) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553665). *Polysphondylium arachnoideum* Vadell & Cavender, Mycologia 99: 120 (2007)

Heterostelium asymetricum (Vadell & Cavender) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553666). *Polysphondylium asymetricum* Vadell & Cavender, Mycologia 90: 719 (1998).

Heterostelium australicum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553667). *Polysphondylium australicum* Cavender et al., Austral. Syst. Bot. 21: 60 (2008)

Heterostelium boreale (Romeralo et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553668). *Dictyostelium boreale* Romeralo et al., Mycologia 102: 592 (2010)

Heterostelium candidum (H.Hagiw.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553669). *Polysphondylium candidum* H.Hagiw., Rep. Tottori Mycol. Inst. 10: 591 (1973)

Heterostelium colligatum (Vadell & Cavender) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553670). *Polysphondylium colligatum* Vadell & Cavender, Mycologia 90: 719 (1998)

Heterostelium cumulocystum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553671). *Polysphondylium cumulocystum* Cavender et al., Mycologia 108: 87 (2016)

Heterostelium equisetoides (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553672). *Polysphondylium equisetoides* Cavender et al., Syst. Geogr. Pl. 74: 248 (2004)

Heterostelium filamentosum (F.Traub et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553673). *Polysphondylium filamentosum* F.Traub et al., Amer. J. Bot. 68: 169 (1981)

Heterostelium flexuosum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553674). *Dictyostelium flexuosum* Cavender et al., Austral. Syst. Bot. 21: 51 (2008)

Heterostelium gloeosporum (H.Hagiw.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553675). *Dictyostelium gloeosporum* H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 29: 127 (2003)

Heterostelium granulosum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553676). *Dictyostelium granulosum* Cavender et al., Austral. Syst. Bot. 21: 55 (2008)

Heterostelium lapidosum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553677). *Polysphondylium lapidosum* Cavender et al., Mycologia 108: 88 (2016)

Heterostelium luridum (G.Kauffm. et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553678). *Polysphondylium luridum* G.Kauffm. et al., Bot. Helv. 98: 125 (1988)

Heterostelium migratissimum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553679). *Polysphondylium migratissimum* Cavender et al., Mycologia 108: 89 (2016)

Heterostelium multicystogenum (S.Kawak. & H.Hagiw.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553680). *Polysphondylium multicystogenum* S.Kawak. & H.Hagiw., Mycologia 100: 347 (2008)

Heterostelium naviculare (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553681). *Dictyostelium naviculare* Cavender et al., Mycologia 97: 504 (2005)

Heterostelium oculare (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553682). *Dictyostelium oculare* Cavender et al., Mycologia 97: 505 (2005)

Heterostelium pallidum (Olive) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553683). *Polysphondylium pallidum* Olive, Proc. Amer. Acad. Arts 37: 341 (1901)

Heterostelium parvimigratum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553684). *Polysphondylium parvimigratum* Cavender et al., Mycologia 108: 90 (2016)

Heterostelium perasymmetricum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553685). *Polysphondylium perasymmetricum* Cavender et al., Mycologia 108: 91 (2016)

Heterostelium plurimicrocystogenum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553686). *Polysphondylium plurimicrocystogenum* Cavender et al., Mycologia 108: 92 (2016)

Heterostelium pseudocandidum (H.Hagiw.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553687). *Polysphondylium pseudocandidum* H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 5: 67 (1979)

Heterostelium pseudocolligatum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553688). *Polysphondylium pseudocolligatum* Cavender et al., Mycologia 108: 94 (2016)

Heterostelium pseudoplasmodiofascium (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553689). *Polysphondylium pseudoplasmodiofascium* Cavender et al., Mycologia 108: 96 (2016)

Heterostelium pseudoplasmodiomagnum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553690). *Polysphondylium pseudoplasmodiomagnum* Cavender et al., Mycologia 108: 97 (2016)

Heterostelium racemiferum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553691). *Polysphondylium racemiferum* Cavender et al., Mycologia 108: 98 (2016)

Heterostelium rotatum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553692). *Dictyostelium rotatum* Cavender et al., Austral. Syst. Bot. 21: 60 (2008)

Heterostelium stolonicoideum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553693). *Polysphondylium stolonicoideum* Cavender et al., Austral. Syst. Bot. 21: 62 (2008)

Heterostelium tenuissimum (H.Hagiw.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553694). *Polysphondylium tenuissimum* H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 5: 69 (1979)

Heterostelium tikalense (Vadell & Cavender) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553695). *Polysphondylium tikalense* Vadell & Cavender, Mycologia 90: 721 (1998), as "*tikaliensis*"

Heterostelium unguliferum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553696). *Polysphondylium unguliferum* Cavender et al., Mycologia 108: 99 (2016)

Heterostelium violaceotypum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553697). *Polysphondylium violaceotypum* Cavender et al., Mycologia 108: 100 (2016)

Cavenderiaceae S.Baldauf, S.Sheikh & Thulin, fam. nov. (Index Fungorum IF553754).

Type: *Cavenderia* S.Baldauf, S.Sheikh & Thulin

Diagnosis: New monogeneric family, sister group of Acytosteliaceae, from which it differs by having in the SSU rRNA gene GT (not AA) in the nucleotide positions 471-472 and CAT (not AGA) in the positions 907-909 of Supplementary Material alignment S5 (Figs 2, 3D).

Description: Sorocarps with cellular stalks, solitary to loosely or (rarely) tightly clustered, unbranched or irregularly branched, white-hyaline or pale yellow. Spores oblong to elliptic or reniform in outline, with consolidated polar or subpolar granules. Microcysts and macrocysts sometimes present. Streaming aggregation, slug migration stalked or stalkless, acrasin unknown.

Cavenderia S.Baldauf, S.Sheikh & Thulin, gen. nov. (Index Fungorum IF553698). **Type:** *Cavenderia fasciculata* (F.Traub et al.) S.Baldauf, S.Sheikh & Thulin (Fig. 7)

Diagnosis: New genus, sister group of *Acytostelium*, *Rostrostelium* and *Heterostelium* together, from all of which it differs by having in the SSU rRNA gene GT (not AA) in the nucleotide positions 482-483 and CAT (not AGA) in the positions 916-918 of Supplementary Material alignment S5 (Figs 2, 3D).

Description: Sorocarps with cellular stalks, solitary to loosely or (rarely) tightly clustered, unbranched or irregularly branched, white-hyaline or pale yellow, mostly 0.2-7 mm high (rarely up to 1 cm). Spores 3.0-8.0 × 1.5-4.0 µm, oblong to elliptic or reniform in outline, with consolidated polar or subpolar granules. Microcysts and macrocysts sometimes present. Streaming aggregation, slug migration stalked or stalkless, acrasin unknown.

Etymology: Named after James C. Cavender, Ohio University, Athens, since the 1960's the author of numerous species of dictyostelids from all over the world and the leading expert in the field.

Cavenderia amphispora (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553699). *Dictyostelium amphisporum* Cavender et al., Mycologia 97: 503 (2005)

Cavenderia antarctica (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553700). *Dictyostelium antarcticum* Cavender et al., New Zealand J. Bot. 40: 245 (2002)

Cavenderia aureostipes (Cavender) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553701). *Dictyostelium aureostipes* Cavender, Amer. J. Bot. 66: 209 (1979)

Cavenderia aureostipes (Cavender) S.Baldauf, S.Sheikh & Thulin var. *helvetia* (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553655). *Dictyostelium aureostipes* Cavender var. *helvetium* Cavender et al., Amer. J. Bot. 66: 209 (1979)

Cavenderia bifurcata (Cavender) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553702). *Dictyostelium bifurcatum* Cavender, Amer. J. Bot. 63: 66 (1976)

Cavenderia boomerangispora (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553703). *Dictyostelium boomerangisporum* Cavender et al., Austral. Syst. Bot. 21: 51 (2008), as "*boomeransporum*"

Cavenderia delicata (H.Hagiw.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553704). *Dictyostelium delicatum* H.Hagiw., Bull. Natl. Sci. Mus., Tokyo 14: 359 (1971)

Cavenderia deminutiva (J.S.Anderson et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553705). *Dictyostelium deminutivum* J.S.Anderson et al., Mycologia 60: 51 (1968)

Cavenderia exigua (H.Hagiw.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553706). *Dictyostelium exiguum* H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 9: 149 (1983)

Cavenderia fasciculata (F.Traub et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553707). *Dictyostelium fasciculatum* F.Traub et al., Amer. J. Bot. 68: 166 (1981)

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Cavenderia fasciculoidea (Vadell et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553708). *Dictyostelium fasciculoideum* Vadell et al., Mycologia 103: 107 (2011)

Cavenderia granulophora (Vadell et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553709). *Dictyostelium granulophorum* Vadell et al., Mycologia 87: 557 (1995)

Cavenderia macrocarpa (Vadell & Cavender) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553710). *Dictyostelium macrocarpum* Vadell & Cavender, Mycologia 99: 113 (2007)

Cavenderia medusoides (Vadell et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553711). *Dictyostelium medusoides* Vadell et al., Mycologia 87: 555 (1995)

Cavenderia mexicana (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553712). *Dictyostelium mexicanum* Cavender et al., Amer. J. Bot. 68: 379 (1981)

Cavenderia microspora (H.Hagiw.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553713). *Dictyostelium microsporum* H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 4: 27 (1978)

Cavenderia multistipes (Cavender) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553714). *Dictyostelium multistipes* Cavender, Amer. J. Bot. 63: 63 (1976)

Cavenderia myxobasis (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553715). *Dictyostelium myxobasis* Cavender et al., Austral. Syst. Bot. 21: 56 (2008)

Cavenderia nanopodium (Vadell & Cavender) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553716). *Dictyostelium nanopodium* Vadell & Cavender, Mycologia 99: 118 (2007)

Cavenderia parvispora (H.Hagiw.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553717). *Dictyostelium parvisporum* H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 12: 99 (1986)

Cavenderia stellata (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553718). *Dictyostelium stellatum* Cavender et al., Mycologia 97: 508 (2005)

Dictyosteliales L.S.Olive ex P.M.Kirk et al., Ainsworth & Bisby's Dictionary of the Fungi, ed. 9: x (2001). **Type:** *Dictyostelium* Bref.

Order comprising the two families Dictyosteliaceae and Raperosteliaceae, and the genus *Coremiostelium* not assigned to family.

Description: Sorocarps with cellular stalks, sometimes with acellular apical stretches, sometimes with crampon-shaped bases, colorless or with white to pale yellow or purple sori, solitary or clustered, unbranched, irregularly branched or sometimes with regularly spaced whorls of branches or coremiform. Spores mostly elliptic or oblong in outline, sometimes globose, granules present or absent. Microcysts and macrocysts sometimes present. Streaming

or non-streaming aggregation, slug migration present or absent, sometimes stalked, acrasin cAMP, glorin, folate, pterin or unknown.

Dictyosteliaceae Rostaf. ex Cooke, Contr. Mycol. Brit.: 53 (1877). **Type:** *Dictyostelium* Bref. Family comprising two genera, *Dictyostelium* and *Polysphondylium*.

Description: Sorocarps with cellular stalks, colorless or with white to pale yellow sori, solitary or clustered, unbranched, irregularly branched, with regularly spaced whorls of branches or coremiform. Spores elliptic or oblong in outline, granules present or absent. Microcysts rare macrocysts more common. Streaming aggregation, slug migration present or absent, sometimes stalked, acrasin cAMP, glorin or unknown.

Dictyostelium Bref., Abh. Senckenberg. Naturf. Ges. 7: 85 (1869). **Type:** *Dictyostelium mucoroides* Bref. (Fig. 8)

= *Hyalostilbum* Oudem., Ned. Kruidk. Arch., ser. 2, 4: 241 (1885). **Type:** *Hyalostilbum sphaerocephalum* Oudem.

Description: Sorocarps with cellular stalks, colorless or with white to pale yellow sori, mostly solitary but sometimes clustered, mostly unbranched but sometimes with irregular branches, generally 3-7 mm in height but >1 cm common (range 1.5-43.0 mm), often with a basal support disk. Spores mostly elliptic or sometimes oblong in outline, polar granules mostly absent and unconsolidated where present, commonly 4.0-9.0 × 2.0-5.0 µm (range 3.0-26.0 ×2.0-7.5 µm). Microcysts rarely observed, macrocysts more common. Streaming aggregation, slug migration stalked or stalkless when present, acrasin cAMP or unknown (likely cAMP).

Dictyostelium ammophilum Romeralo et al. ex S.Baldauf, S.Sheikh & Thulin, sp. nov. (Index Fungorum IF553657). **Holotype:** U.S.A., Alaska, isolate NW2B, Landolt #864 (stored in liquid nitrogen at the Dicty Stock Center, strain ID DBS0349823)

Note on typification: *Dictyostelium ammophilum* was described and illustrated by Romeralo et al. in Mycologia 102: 590 (2010), and the isolate NW2B, Landolt #864 was cited as holotype. However, in p. 592 of this paper Romeralo et al. state that this isolate "will be deposited at the American Type Culture Collection (ATCC) and/or the Dicty Stock Center". This is contrary to ICN Art. 40.7 (McNeill et al. 2012), which states that for valid publication of names of new species published after 1 January 1990 "the single herbarium or collection or

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institution in which the type is conserved must be specified". We therefore here validate *D. ammophilum* by designation of the isolate in Dicty Stock Center strain ID DBS0349823 as holotype.

Dictyostelium aureocephalum H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 17: 103 (1991)

Dictyostelium aureum Olive, Proc. Amer. Acad. Arts 37: 340 (1901)

Dictyostelium aureum Olive var. *luteolum* Cavender et al., Amer. J. Bot. 68: 376 (1981)

Dictyostelium austroandinum Vadell et al., Mycologia 103: 103 (2011)

Dictyostelium barbibulus Perrigo & Romeralo, Fung. Diversity 58: 191 (2013)

Dictyostelium brefeldianum H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 10: 39 (1984)

Dictyostelium brevicaule Olive, Proc. Amer. Acad. Arts 37: 340 (1901)

Dictyostelium brunneum Kawabe, Trans. Mycol. Soc. Japan 23: 91 (1982)

Dictyostelium capitatum H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 9: 45 (1983)

Dictyostelium chordatum Vadell et al., Mycologia 103: 105 (2011)

Dictyostelium citrinum Vadell et al., Mycologia 87: 553 (1995)

Dictyostelium clavatum H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 18: 1 (1992)

Dictyostelium crassicaule H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 10: 67 (1984)

Dictyostelium dimigraformum Cavender, J. Gen. Microbiol. 62: 115 (1970)

Dictyostelium discoideum Raper, J. Agric. Res. 50: 135 (1935)

Dictyostelium firmibasis H.Hagiw., Bull. Natl. Sci. Mus., Tokyo 14: 356 (1971)

Dictyostelium gargantuum Vadell et al., Mycologia 103: 108 (2011)

Dictyostelium giganteum B.N.Singh, J. Gen. Microbiol. 1: 17 (1947)

Dictyostelium implicatum H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 10: 63 (1984)

Dictyostelium intermedium Cavender, Amer. J. Bot. 63: 63 (1976)

Dictyostelium leptosomopsis Vadell et al., Mycologia 103: 110 (2011)

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Dictyostelium leptosomum Cavender et al., New Zealand J. Bot. 40: 252 (2002)

Dictyostelium longosporum H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 9: 55 (1983)

Dictyostelium macrocephalum H.Hagiw. et al., Bull. Natl. Sci. Mus., Tokyo, B 11: 104 (1985)

Dictyostelium medium H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 18: 4 (1992)

Dictyostelium mucoroides Bref., Abh. Senckenberg. Naturf. Ges. 7: 85 (1869)

Dictyostelium mucoroides Bref. var. *stoloniferum* Cavender & Raper, Amer. J. Bot. 55: 510 (1968)

Dictyostelium pseudobrefeldianum H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 22: 47 (1996)

Dictyostelium purpureum Olive, Proc. Amer. Acad. Arts 37: 340 (1901)

Dictyostelium quercibrachium Cavender et al., New Zealand J. Bot. 40: 258 (2002)

Dictyostelium robustum H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 22: 51 (1996)

Dictyostelium rosarium Raper & Cavender, J. Elisha Mitchell Sci. Soc. 84: 31 (1968)

Dictyostelium septentrionale Cavender, Canad. J. Bot. 56: 1329 (1978), as "*septentrionalis*"

Dictyostelium sphaerocephalum (Oudem.) Sacc. & Marchal, Bull. Soc. Roy. Bot. Belgique 24: 74 (1885). *Hyalostilbum sphaerocephalum* Oudem., Ned. Kruidk. Arch., ser. 2, 4: 241 (1885)

Dictyostelium valdivianum Vadell et al., Mycologia 103: 111 (2011)

Polysphondylium Bref., Untersuch. Gesammt. Mycol. 6: 5 (1884). **Type:** *Polysphondylium violaceum* Bref. (Fig. 9)

Description: Sorocarps with cellular stalks and sori pigmented violet/lavender/purple often darkening with age, whorls of branches regularly or irregularly spaced, clustered or solitary, height 1-20 mm. Spores mostly ellipsoid with polar granules often consolidated, 5.0-12.5 × 2.5-5.0 µm. Macrocysts sometimes observed, microcysts unknown. Streaming aggregation, slug migration stalked when present, acrasin glorin or unknown.

Polysphondylium fuscans Perrigo & Romeralo, Fung. Diversity 58: 192 (2012)

Polysphondylium laterosorum (Cavender) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553719). *Dictyostelium laterosorum* Cavender, J. Gen. Microbiol. 62: 117 (1970)

Polysphondylium patagonicum Vadell et al., Mycologia 103: 113 (2011)

Polysphondylium violaceum Bref., Untersuch. Gesammt. Mycol. 6: 5 (1884)

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Raperosteliaceae S.Baldauf, S.Sheikh & Thulin, fam. nov. (Index Fungorum IF553755). **Type:** *Raperostelium* S.Baldauf, S.Sheikh & Thulin

Diagnosis: New family differing from Dictyosteliacae and *Coremiostelium* by having in the SSU rRNA gene CAA (not CGA) in the nucleotide positions 1050-1052 and ATC (not ACC) in the positions 1391-1393 of Supplementary Material alignment S6 (Figs 2, 3E).

Family comprising four genera, *Speleostelium*, *Tieghemostelium, Hagiwaraea* and *Raperostelium*.

Description: Sorocarps with cellular stalks, sometimes with acellular apical stretches, colorless, solitary or clustered, sometimes with crampon-shaped bases, unbranched or with irregularly spaced branches. Spores ellipsoid to globose or oblong, granules present or absent. Microcysts sometimes present, macrocysts rare or unknown. Non-streaming or streaming aggregation, slug migration present or absent, sometimes stalked, acrasin glorin, folate, pterin or unknown.

Speleostelium S.Baldauf, S.Sheikh & Thulin, gen. nov. (Index Fungorum IF553748). **Type:** *Speleostelium caveatum* (Waddell et al.) S.Baldauf, S.Sheikh & Thulin (Fig. 10)

Diagnosis: New genus, sister to *Tieghemostelium, Hagiwaraea* and *Raperostelium* together, differing from all of them by having in the SSU rRNA gene GCA (not TTT) in the nucleotide positions 201-203 and CG (not TA) in the positions 1093-1094 of Supplementary Material alignment S7 (Figs 2, 11A).

Description: Sorocarps with cellular stalks, delicate, colorless, typically clustered, erect or semi-erect, 3-7 mm high, often tangled. Spores ellipsoid, 2.7 × 7.8 µm, prominent granules usually but not consistently polar. Microcysts and macrocysts

unknown. Non-streaming aggregation, no slug migration, acrasin glorin. Myxamoebae prey upon cells of other dictyostelids and prevent them from fruiting.

Etymology: "Speleo-" in the name refers to the fact that the single species known in the genus is cave-dwelling.

Speleostelium caveatum (Waddell et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553720). *Dictyostelium caveatum* Waddell et al. in Raper, The dictyostelids: 311 (1984)

Hagiwaraea S.Baldauf, S.Sheikh & Thulin, gen. nov. (Index Fungorum IF553749). **Type:** *Hagiwaraea rhizopodium* (Raper & Fennell) S.Baldauf, S.Sheikh & Thulin (Fig. 12)

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Diagnosis: New genus, sister group of *Raperostelium*, from which it differs by having sorocarps with a crampon-shaped (not simple) base and by having in the SSU rRNA gene GTTGGCTCG (not ATTGGTTGC) in the nucleotide positions 866-874 and GAGTA (not CGGTA) in the positions 1462-1466 of Supplementary Material alignment S8 (Figs 2, 11B).

Description: Sorocarps with cellular stalks, colorless, with digitate crampon-like bases, solitary or clustered, typically unbranched or rarely with sparse irregularly spaced branches, mostly delicate, 0.3-7 mm, but reach 1.5 cm in stoloniferous form of *H. vinaceofusca*. Spores generally oblong, with consolidated polar granules (absent in *H. vinaceofusca*), mostly 5.0-12 ×2.5-4.5 µm. Microcysts commonly observed, macrocysts unknown. Streaming aggregation, slug migration stalked, acrasin unknown.

Etymology: Named after Hiromitsu Hagiwara, Tokyo, author of many species of dictyostelids, particularly from Japan and other Asian countries.

Hagiwaraea coeruleostipes (Raper & Fennell) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553721). *Dictyostelium coeruleostipes* Raper & Fennell, Amer. J. Bot. 54: 519 (1967)

Hagiwaraea lavandula (Raper & Fennell) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553722). *Dictyostelium lavandulum* Raper & Fennell, Amer. J. Bot. 54: 519 (1967)

Hagiwaraea radiculata (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553723). *Dictyostelium radiculatum* Cavender et al., Austral. Syst. Bot. 21: 57 (2008)

Hagiwaraea rhizopodium (Raper & Fennell) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553724). *Dictyostelium rhizopodium* Raper & Fennell, Amer. J. Bot. 54: 517 (1967)

Hagiwaraea vinaceofusca (Raper & Fennell) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553725). *Dictyostelium vinaceofuscum* Raper & Fennell, Amer. J. Bot. 54: 522 (1967)

Raperostelium S.Baldauf, S.Sheikh & Thulin, gen. nov. (Index Fungorum IF553750). **Type:** *Raperostelium minutum* (Raper) S.Baldauf, S.Sheikh & Thulin (Fig. 13)

Diagnosis: New genus, sister group of *Hagiwaraea*, from which it differs by having sorocarps with a simple (not crampon-shaped) base and by having in the SSU rRNA gene ATTGGTTGC (not GTTGGCTCG) in the nucleotide positions 866-874 and CGGTA (not GAGTA) in the positions 1462-1466 of Supplementary Material alignment S9 (Figs 2, 11C).

Description: Sorocarps with cellular stalks, colorless, solitary or clustered, branches absent to irregularly whorled, delicate, 0.5-7 mm in height, base simple or clavate. Spores oblong or elliptic in outline, granules inconsistently present/consolidated/polar, 4.0-10.0 × 1.8-5.0 µm, highly variable in some species. Microcysts commonly observed, macrocysts known only for *R. minutum.* Aggregation streaming minor or absent, slug migration present or absent, acrasin folate (*R. minutum*) or unknown.

Etymology: Named after Kenneth Bryan Raper (1908-1987), author of "The Dictyostelids" (Raper 1984), a landmark in the field, and author of numerous species of dictyostelids, including the type of *Raperostelium*.

Raperostelium australe (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553726). *Dictyostelium australe* Cavender et al., New Zealand J. Bot. 40: 249 (2002)

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Raperostelium capillare (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553727). *Dictyostelium capillare* Cavender et al., Mycologia 105: 617 (2012)

Raperostelium filiforme (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553728). *Dictyostelium filiforme* Cavender et al., Mycologia 105: 619 (2012)

Raperostelium gracile (H.Hagiw.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553729). *Dictyostelium gracile* H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 9: 150 (1983)

Raperostelium ibericum (Romeralo et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553730). *Dictyostelium ibericum* Romeralo et al., Mycologia 101: 270 (2009)

Raperostelium maeandriforme (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553731). *Dictyostelium maeandriforme* Cavender et al., Mycologia 105: 621 (2012)

Raperostelium minutum (Raper) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553732). *Dictyostelium minutum* Raper, Mycologia 33: 634 (1941)

Raperostelium monochasioides (H.Hagiw.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553733). *Dictyostelium monochasioides* H.Hagiw., Bull. Natl. Sci. Mus., Tokyo 16: 494 (1973)

Raperostelium ohioense (Cavender & Vadell) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553734). *Dictyostelium ohioense* Cavender & Vadell, Bull. Ohio Biol. Surv., n.s. 16: 29 (2006)

Raperostelium potamoides (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553735). *Dictyostelium potamoides* Cavender et al., Mycologia 97: 507 (2005)

Raperostelium reciprocatum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553736). *Dictyostelium reciprocatum* Cavender et al., Mycologia 105: 622 (2012)

Raperostelium reciprocatum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin var. *transitum* (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553656). *Dictyostelium reciprocatum* Cavender et al. var. *transitum* Cavender et al., Mycologia 105: 629 (2012)

Raperostelium tenue (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553737). *Dictyostelium tenue* Cavender et al., Amer. J. Bot. 66: 213 (1979)

Tieghemostelium S.Baldauf, S.Sheikh & Thulin, gen. nov. (Index Fungorum IF553751).

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Type: *Tieghemostelium lacteum* (Tiegh.) S.Baldauf, S.Sheikh & Thulin (Fig. 14)

Diagnosis: New genus, sister group of *Hagiwaraea* and *Raperostelium* together, from both of which it differs by having in the SSU rRNA gene GCAA (not TCCG, TTCG, TTTG or CTCG) in the nucleotide positions 246-249 and CGA (not AGG or GGG) in the positions 511-513 of Supplementary Material alignment S10 (Figs 2, 11D).

Description: Sorocarps with cellular stalks, sometimes with an acellular apical stretch, colorless, delicate, 0.3-2.5 mm high, base simple or clavate, solitary or clustered, branches absent or sparse and irregular. Spore shape variable (ellipsoid/oblong/globose), likewise granule presence/absence and arrangement, 3.5-11.0 ×1.8-4.8 µm. Microcysts known for most species, macrocysts known for *T. lacteum* (D. Anderson and J. Cavender, unpublished). Non-streaming aggregation, slug migration present or absent, acrasin pterin (*T. lacteum*) or unknown.

Etymology: Named after Philippe Édouard Léon van Tieghem (1839-1914), French botanist and mycologist, to whom "we owe our first clear insight into the true and unique nature of the so-called cellular slime molds" (Raper 1984), and who is the author of several species of dictyostelids and other sorocarpic amoebae, including the type of *Tieghemostelium*.

Tieghemostelium angelicum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553738). *Dictyostelium angelicum* Cavender et al., Mycologia 105: 624 (2012)

Tieghemostelium dumosum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553739). *Dictyostelium dumosum* Cavender et al., Mycologia 105: 627 (2012)

Tieghemostelium lacteum (Tiegh.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553740). *Dictyostelium lacteum* Tiegh., Bull. Soc. Bot. France, Mém. 27: 320 (1880)

Tieghemostelium lacteum (Tiegh.) S.Baldauf, S.Sheikh & Thulin var. *papilloideum* (Cavender) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553741). *Dictyostelium lacteum* Tiegh. var. *papilloideum* Cavender, Amer. J. Bot. 63: 68 (1976)

Tieghemostelium menorah (Vadell & Cavender) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553742). *Dictyostelium menorah* Vadell & Cavender, Mycologia 99: 117 (2007)

Tieghemostelium montium (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553743). *Dictyostelium montium* Cavender et al., Mycologia 105: 625 (2012)

Tieghemostelium simplex (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553744). *Dictyostelium simplex* Cavender et al., Mycologia 105: 614 (2012)

Tieghemostelium unicornutum (Cavender et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553745). *Dictyostelium unicornutum* Cavender et al., Mycologia 105: 616 (2012)

Genus of Dictyosteliales not Assigned to Family

Coremiostelium S.Baldauf, S.Sheikh, Thulin & Spiegel, gen. nov. (Index Fungorum IF553752). **Type:** *Coremiostelium polycephalum* (Raper) S.Baldauf, S.Sheikh & Thulin (Fig. 15)

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Diagnosis: New genus differing from *Dictyostelium, Hagiwaraea, Polysphondylium, Raperostelium, Speleostelium* and *Tieghemostelium* by having the stalks of the sorocarps forming a single column and diverging only terminally, and by having in the SSU rRNA gene TAAA (not CAAG, CAAT, GAAG or CAAA) in the nucleotide positions 187-190 and CCAG (not TTAA, TTAG, TTGA, GCGG, CTAT, TTAC, ATAA or ATAG) in the positions 1129-1132 of Supplementary Material alignment S11 (Figs 2, 11E).

Description: Sorocarps with cellular stalks, colorless, 0.35-0.65 mm in height, typically coremiform and adherent along most of their length and diverging only terminally. Microcysts common, macrocysts informally reported. Spores elliptic to reniform in outline, 6.0-7.5 × 3.0-3.5 µm, granules often present but not consistently polar. Streaming aggregation, slug migration stalkless, acrasin unknown.

Etymology: The name alludes to the typically coremiform fructifications with the stalks of the sorocarps adherent along most of their length.

Note: According to the results of Singh et al. (2016), *Coremiostelium* would be a member of Dictyosteliaceae.

Coremiostelium polycephalum (Raper) S.Baldauf, S.Sheikh, Thulin & Spiegel, comb. nov. (Index Fungorum IF553746). *Dictyostelium polycephalum* Raper, J. Gen. Microbiol. 14: 717 (1956)

Genus not Assigned to Family or Order

Synstelium S.Baldauf, S.Sheikh & Thulin, gen. nov. (Index Fungorum IF553753). **Type:** *Synstelium polycarpum* (F.Traub et al.) S.Baldauf, S.Sheikh & Thulin (Fig. 16)

Diagnosis: New genus differing from all other dictyostelids by having in the SSU rRNA gene TCTA (not TTCG, TTCA, TTCT, TTTA, TAAA, TGGT, ACTC, TCAC, etc) in the nucleotide positions 270-273 and CAATTT (not CAGTAT, CAATAT, TAACAC, TAATAC, etc) in the positions 607-612 of Supplementary Material alignment S12 (Figs 2, 11F).

Description: Sorocarps with cellular stalks, unbranched, clustered and adherent over lower 1/3 of final height, colorless or with faint yellow stalk, typically 3-7 mm in height. Spores 7.8 × 2.7 µm, reniform to elliptic in outline, with loosely arranged polar granules. Microcysts and macrocysts unknown. Streaming aggregation, no slug migration, acrasin unknown.

Etymology: The prefix "syn-" refers to the clustered sorocarps with the stalks adherent near the base.

Note: According to the results of Singh et al. (2016), *Synstelium* would be a member of Acytosteliaceae.

Synstelium polycarpum (F.Traub et al.) S.Baldauf, S.Sheikh & Thulin, comb. nov. (Index Fungorum IF553747). *Dictyostelium polycarpum* F.Traub et al., Amer. J. Bot. 68: 164 (1981)

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Species incertae sedis

Dictyostelium arabicum H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 17: 110 (1991)

Dictyostelium culliculosum Yu Li & Xiao L.He, Mycotaxon 106: 380 (2008)

Dictyostelium dichotomum Vadell & Cavender, Mycologia 99: 116 (2007)

Dictyostelium germanicum Cavender et al., Bot. Helv. 105: 201 (1995)

Dictyostelium globisporum Yu Li & Pu Liu, Mycologia 103: 641 (2011)

Dictyostelium irregulare L.S.Olive et al., Amer. J. Bot. 54: 354 (1967), as "*irregularis*"

Dictyostelium magnum H.Hagiw., Bull. Natl. Sci. Mus., Tokyo, B 9: 155 (1983)

Dictyostelium microsorocarpum Yu Li & Xiao L.He, Mycotaxon 111: 287 (2010)

Dictyostelium roseum Tiegh., Bull. Soc. Bot. France 27: 320 (1880)

Dictyostelium vermiforme Vadell & Cavender, Mycologia 99: 118 (2007), as "*vermiformum*"

Genus incertae sedis

Coenonia Tiegh., Bull. Soc. Bot. France 31: 304 (1884). **Type:** *Coenonia denticulata* Tiegh.

Coenonia denticulata has never been recollected, but the crampon-shaped base described for this species has been compared with the basal support found in species here treated as members of *Hagiwaraea*. However, some other features, such as the cupule-like structure with a finely dentate rim said to surround the spores in *C. denticulata,* have no parallel among members of *Hagiwaraea*, or among other known dictyostelids (Raper 1984). *Coenonia* therefore remains an enigma and may or may not be a dictyostelid.

Methods

The new classification is based on SSU rRNA gene phylogeny (Romeralo et al. 2011; Schaap et al. 2006; Supplementary Material Fig. S1). The one exception is the root, which is not resolved by SSU rRNA (Schaap et al 2006), but is strongly and consistently supported by multi-protein phylogeny (Romeralo et al. 2014; Sheikh et al. 2015; Singh et al. 2016). Taxon naming is made according to the International Code of Nomenclature for algae, fungi, and plants (ICN) (McNeill et al. 2012), and the use of molecular characters as taxon diagnostics follows the guidelines proposed by Tripp and Lendemer (2014).

Molecular characters for group diagnoses utilized SSU rRNA with sequences aligned for all taxa and for specific groups using MUSCLE (Edgar 2004) with default settings as implemented in AliView (V1.19-beta-3, Larsson 2014). These alignments were further refined by eye to correct for obvious errors that are inevitable in automated SSU rRNA alignment (e.g. Cole et al. 2014). The full alignment and group-specific alignments are provided as supplementary data (Supplementary Material Figs S2-S13, respectively). Two molecular synapomorphies were chosen for each new taxon diagnosis, and the full set of synapomorphies for each group is shown in Supplementary Material Table S1. Diagnostic morphological characters were added where available and for all genera, families and orders brief morphological descriptions are given using the full range of original species descriptions.

Phylogenetic reconstruction of the SSU rRNA tree (Supplementary Material Fig. S13) utilized the full SSU rRNA alignment manually trimmed to remove poorly aligned regions, yielding 1560 universally aligned positions (indicated on Supplementary Material Fig. S13). Phylogenetic analyses were conducted using RAxML (V7.2.8, Stamatakis 2006) with the GTR substitution model and a gamma correction for rate variation among sites (GTRGAMMA). Clade support was determined using the same method and model for 1000 bootstrap replicates. Analyses including all sequences strongly support the extremely divergent *Cavenderia multistipes* and *C. nanopodium* sequences as members of the genus *Cavenderia*. These sequences were then deleted from the final analysis as such disproportionately long branches tend to interfere with accurate tree reconstruction due to the problem of long branch attraction (Bergsten 2005).

Acknowledgements

We thank Alastair Simpson and Pauline Schaap for helpful comments on the manuscript. We also thank the Discover Life webserver (www.discoverlife.org/) for easy access to many original species descriptions and the Cyberinfrastructure for Phylogenetic Research (CIPRES) for the use of computational resources.

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Figure Legends

Figure 1. Schematic overview of dictyostelid phylogeny and new taxonomy. The figure shows all dictyostelid major groups that receive consistent and strong statistical support from SSU rRNA phylogeny (Romeralo et al. 2011; Schaap et al. 2006; Supplementary Material Fig. S1). The root, which is not well resolved by SSU rRNA (Schaap et al. 2006), is based on three separate multi-protein phylogenies (Romeralo et al. 2014; Sheikh et al. 2015; Singh et al. 2016). New names proposed herein are indicated in red.

Figure 2. Schematic diagram of the dictyostelid SSU rRNA alignment indicating regions carrying taxonomic signatures. Dictyostelid-wide conserved blocks are indicated in grey and labeled with upper case letters, while variable regions are indicated in red with lower case letters. Regions containing molecular signatures are indicated with arrows pointing to the list of taxa with signatures in the respective region. The positions refer to the global alignment shown in Figure S13. The numbers represent start and end positions of the conserved regions used for global dictyostelid phylogeny (Supplementary Material Fig. S1).

Figure 3. SSU rRNA molecular signatures for dictyostelid taxa. Sequence signatures were extracted from alignments of strict consensus sequences for the relevant taxa (Supplementary Material files S2-S6). Alignment segments carrying signatures, which are highlighted with dark background color, are shown for **A**. Acytosteliales, **B**. *Rostrostelium*, **C**. *Heterostelium*, **D**. *Cavenderia* and Cavenderiaceae, and **E**. Raperosteliaceae. Coordinates are given above each segment indicating the position of the segment within its group-specific alignment (Supplementary Material file indicated at the top). The segment's corresponding region in the global alignment is given at the bottom of each segment and refers to the region designated in Figure 2 and Supplementary Material alignment S13.

Figure 4. *Acytostelium leptosomum*, type of *Acytostelium* (type strain FG-12). **A**. Aggregation. **B**. Cluster of sorogens. **C**. Late sorogen. **D**. Base. **E**. Tip. **F**. Myxamoebae. **G**. Spores. **H**. Sorocarps. Scale bars: A =1 mm; B, C = 100 μm; D-G = 6 μm; H = 0.5 mm. Reproduced from Cavender and Vadell (2000) with permission from Taylor & Francis Ltd (www.tandfonline.com).

Figure 5. *Rostrostelium ellipticum*, type of *Rostrostelium* (type strain AE-2)**. A.** Aggregation. **B**. Cluster of early and late sorogens. **C**, **D**. Narrowed late sorogens. **E**. Myxoamoebae. **F**. Spores. **G**. Sorocarps. Scale bars: A = 100 μm; B-D = 100 μm; E, F = 6 μm; G = 150 μm. Reproduced from Cavender and Vadell (2000) with permission from Taylor & Francis Ltd (www.tandfonline.com).

Figure 6. *Heterostelium pallidum*, type of *Heterostelium* (strain NZ77A)**. A**. Aggregation. **B**. Late pseudoplasmodia. **C**. Base. **D**. Early and late sorogens. **E**. Tips. **F**. Elliptical spores with unconsolidated polar granules. **G**. Myxamoebae. **H**. Solitary and tightly clustered sorocarps. **I**. Whorl. Scale bars: A, B, D = 0.4 mm; C = 20 μm; E, I = 10 μm; F, G = 8 μm; H = 1mm. Reproduced from Cavender et al. (2002) with permission from Taylor & Francis Ltd (www.tandfonline.com).

Figure 7. *Cavenderia fasciculata*, type of *Cavenderia* (strain NZ155B)**. A.** Two patterns of aggregation: large streams, finely fragmented, and a small crateriform late aggregation. **B**, **C**. Solitary (left) and clustered (right), early (**B**) and late (**C**) sorogens. **D**. Clavate base. **E**. Capitate tips. **F**. Elliptical spores with consolidated polar granules. **G.** Myxamoebae. **H**. Solitary unbranched sorocarp. **I**. Clustered branched sorocarp with small young sorogens surrounding bases. Scale bars: A-C =0.5 μm; D = 20 μm; E = 10 μm; F = 5 μm; G = 15 μm;

H, I = 0.5 mm. Reproduced from Cavender et al. (2002) with permission from Taylor & Francis Ltd (www.tandfonline.com).

Figure 8. *Dictyostelium mucoroides*, type of *Dictyostelium.* **A**. Aggregation. **B**. Spores. **C-D**. Tip formation and spores. **E-G**. Sorocarps. Scale bars: A = 0.5 mm; B, C, D = 10 μm; E, F, G = 1 mm (Photos by A. Swanson and F. Spiegel).

Figure 9. *Polysphondylium violaceum*, type of *Polysphondylium* (strain NZ16B). **A**. Large aggregation. **B**. Early and late sorogens in a cluster. **C**. Clustered and solitary sorocarps as seen reacting to light. **D**. Base. **E**. Tip. **F**. Elliptical spores with consolidated polar granules. **G**. Myxamoebae. Scale bars: A, B = 1 mm; C = 2 mm; D, E = 25 μm; F = 5 μm; G = 15 μm. Reproduced from Cavender et al. (2002) with permission from Taylor & Francis Ltd (www.tandfonline.com).

Figure 10. *Speleostelium caveatum*, type of *Speleostelium* (type strain B4-3). **A**. Clustered sorocarps. **B**. Spores containing prominent granules. **C**. Vegetative myxamoebae. **D**. Young aggregations formed without inflowing streams. **E**. Sorocarps of the smaller type (larger type not illustrated). F. Sorophores. For magnification, see Raper (1984). Reproduced from Raper (1984) with permission from Princeton University Press.

Figure 11. SSU rDNA molecular signatures for dictyostelid taxa. Sequence signatures were extracted from alignments of strict consensus sequences for the relevant taxa (Supplementary Material files S7-S12). Alignment segments carrying signatures, which are highlighted with dark background color, are shown for **A**. *Speleostelium*, **B**. *Hagiwaraea*, **C**. *Raperostelium*, **D**. *Tieghemostelium*, **E**. *Coremiostelium* and **F**. *Synstelium*. Coordinates are given above each segment indicating the position of the segment within its group-specific alignment (Supplementary Material file indicated at the top). The segment's corresponding region in the global alignment is given at the bottom of each segment and refers to the region designated in Figure 2 and Supplementary Material S13. The blocked lines show the start and end of the denoted alignment region, and the arrows show continuation of the region.

Figure 12. *Hagiwaraea rhizopodium*, type of *Hagiwaraea* (type strain Pan-33). **A**. Sorocarps. **B**. Spores containing obvious polar granules. **C**. Vegetative myxamoebae. **D**. Two characteristic aggregations. **E**. Larger aggregation; note that inflowing streams have broken up in subcentral area. Fruiting by such dissociated myxamoebae must await emergence of new centers. **F**. Apical area of developing sorocarp showing terminally expanded sporophore

sheath and characteristic orientation of myxamoebae that surround it. **G**. Crampon base and sporophore showing similar differentiation of constituent cells. **H**. Clustered sorogens arising from a single aggregation. **I**. Mature sorocarps of the same strain and young sorogens along colony edge (below). For magnification, see Raper (1984). Reproduced from Raper (1984) with permission from Princeton University Press.

Figure 13. *Raperostelium minutum*, type of *Raperostelium.* **A**. Aggregation. **B**. Spores. **C**, **E**. Sorocarps. **D**. Tip formation. Scale bars: A = 0.5 mm; B = 10 μm; C = 1 mm; D = 10 μm; E = 5mm (Photos by A. Swanson and F. Spiegel)..

Figure 14. *Tieghemostelium lacteum*, type of *Tieghemostelium* (strain UI-14)**.** **A**. Sorocarps. **B**. Vegetative myxamoebae. **C**. Small, mound-like aggregations formed without stream. Insert, aggregation via streams. **D**. Multiple sorogens arising from a single small aggregation. **E**. Three aggregation areas from which multiple, thin sorogens are developing. **F**. A single sorogen in process of fruiting. **G**. Typical sporophore composed of a single tier of vacuolated cells. **H**. Base of clustered sorocarps showing cellular structure. **I**. Bases of sorocarps photographed to show expanded aprons of slime that anchor structures of substrate. **J**. Globose spores characteristic of this species. For magnification, see Raper (1984). Reproduced from Raper (1984) with permission from Princeton University Press.

Figure 15. *Coremiostelium polycephalum*, type of *Coremiostelium* (type strain S-4)**.** **A**. Coremiform sorocarps and newly formed pseudoplasmodia. **B**. Sorocarps. **C**. Spores, showing characteristic shape and commonly a single polar granule. **D**. Myxamoebae beneath coverglass; note empty spore case (arrow) and how it was broken to release the protoplast. **E**. A developing cell aggregation showing typical radial pattern. **F**. Aggregation at edge of a bacterial streak; note ridges that reflect waves of converging myxamoebae. **G**. Aggregations in process of formation (left) and delicate migrating pseudoplasmodia emerging from two centers of aggregation (right). **H**. Two typical migrating pseudoplasmodia. **I**. Migrating pseudoplasmodium. For magnification, see Raper (1984). Reproduced from Raper (1984) with permission from Princeton University Press.

Figure 16. *Synstelium polycarpum*, type of *Synstelium* (type strain GR-4)**.** **A**. Spores showing narrow elliptical form and unconsolidated polar granules. **B**. Vegetative myxamoebae. **C**. Aggregations. **D**. Late aggregates with many papillae. **E**. Sorogens beginning to form. **F**. Field of clustered sorocarps; note diverging sorogens at lower right. For magnification, see

Raper (1984). Reproduced from Raper (1984) with permissions from Princeton University Press.

Appendix A. Supplementary Data

Table S1. Molecular synapomorphies (signatures) using SSU rRNA for each group using sequences in Supplementary Material Figures S2-S12.

Figure S1. Global phylogeny of dictyostelids using universally aligned regions of SSU rDNA. The tree shown was derived by maximum likelihood analysis of 1560 universally aligned SSU rDNA positions (Fig. 2; Supplementary Material file S13). Analyses were conducted using RAxML (version 7.2.8) with the GTR substitution model and a gamma correction for rate variation among sites (GTRGAMMA), with 1000 bootstrap replicates. Taxa are shown with their revised names followed by strain and GenBank accession number for their SSU sequences. Colours are used to indicate the different genera. Bootstrap support values above 50% shown on the relevant branches.

Figure S2. Group-specific SSU rDNA sequence alignment for Acytosteliales. Sequences were aligned using MUSCLE (Edgar 2004) with default settings using the program AliView (version 1.9-beta-3) (Larsson 2004) followed by manual correction of obvious errors.

Figure S3. Group-specific SSU rDNA sequence alignment for *Rostrostelium*. Sequences were aligned as described in Supplementary Material Figure S2.

Figure S4. Group-specific SSU rDNA sequence alignment for *Heterostelium*. Sequences were aligned as described in Supplementary Material Figure S2.

Figure S5. Group-specific SSU rDNA sequence alignment for Cavenderiaceae and *Cavenderia*. Sequences were aligned as described in Supplementary Material S2.

Figure S6. Group-specific SSU rDNA sequence alignment for Raperosteliaceae. Sequences were aligned as described in Supplementary Material Figure S2.

Figure S7. Group-specific SSU rDNA sequence alignment for *Speleostelium*. Sequences were aligned as described in Supplementary Material Figure S2.

Figure S8. Group-specific SSU rDNA sequence alignment for *Hagiwaraea*. Sequences were aligned as described in Supplementary Material Figure S2.

Figure S9. Group-specific SSU rDNA sequence alignment for *Raperostelium*. Sequences were aligned as described in Supplementary Material Figure S2.

Figure S10. Group-specific SSU rDNA sequence alignment for *Tieghemostelium*. Sequences were aligned as described in Supplementary Material Figure S2.

Figure S11. Group-specific SSU rDNA sequence alignment for *Coremiostelium*. Sequences were aligned as described in Supplementary Material Figure S2.

Figure S12. Group-specific SSU rDNA sequence alignment for *Synstelium*. Sequences were aligned as described in Supplementary Material Figure S2.

Figure S13. Master alignment of all dictyostelid SSU rDNA sequences. Sequences were aligned using MUSCLE (Edgar 2004) with default settings using the program AliView (version 1.19-beta-3) (Larsson 2014) followed by manual correction of obvious errors. The top row in the alignment files indicates conserved regions used for phylogeny with capital letter designations and highly variable regions that were excluded with lower case letters. Variable regions consisting of less than six alignment columns are not shown.

Figure1

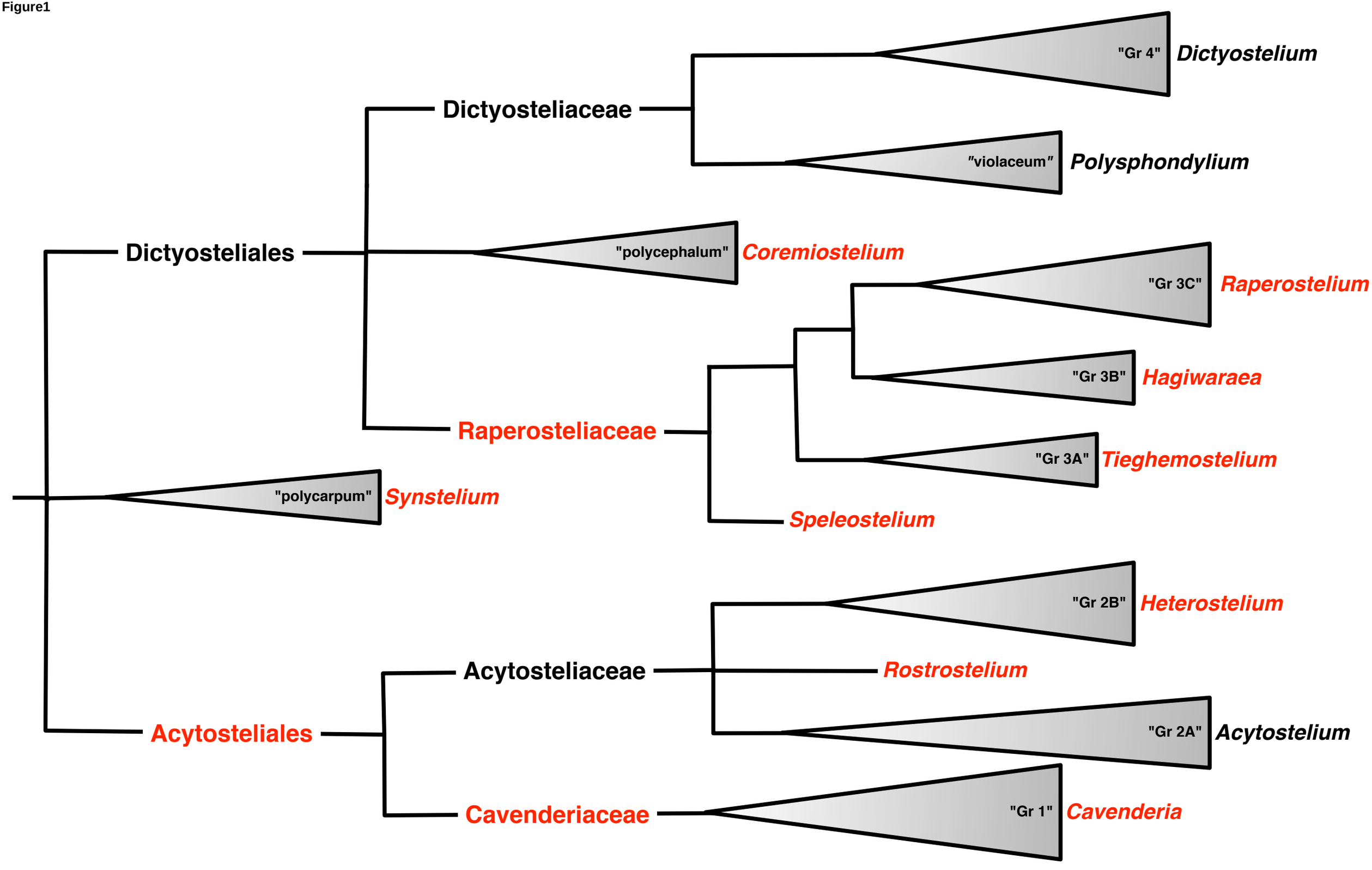

Dictyosteliaceae
"Gr 4"
Dictyostelium
"violaceum"
Polysphondylium
Dictyosteliales
"polycephalum"
Coremiostelium
"Gr 3C"
Raperostelium
"Gr 3B"
Hagiwaraea
Raperosteliaceae
"Gr 3A"
Tieghemostelium
"polycarpum"
Synstelium
Speleostelium
"Gr 2B"
Heterostelium
Acytosteliaceae
Rostrostelium
"Gr 2A"
Acytostelium
Acytosteliales
Cavenderiaceae
"Gr 1"
Cavenderia

Figure2

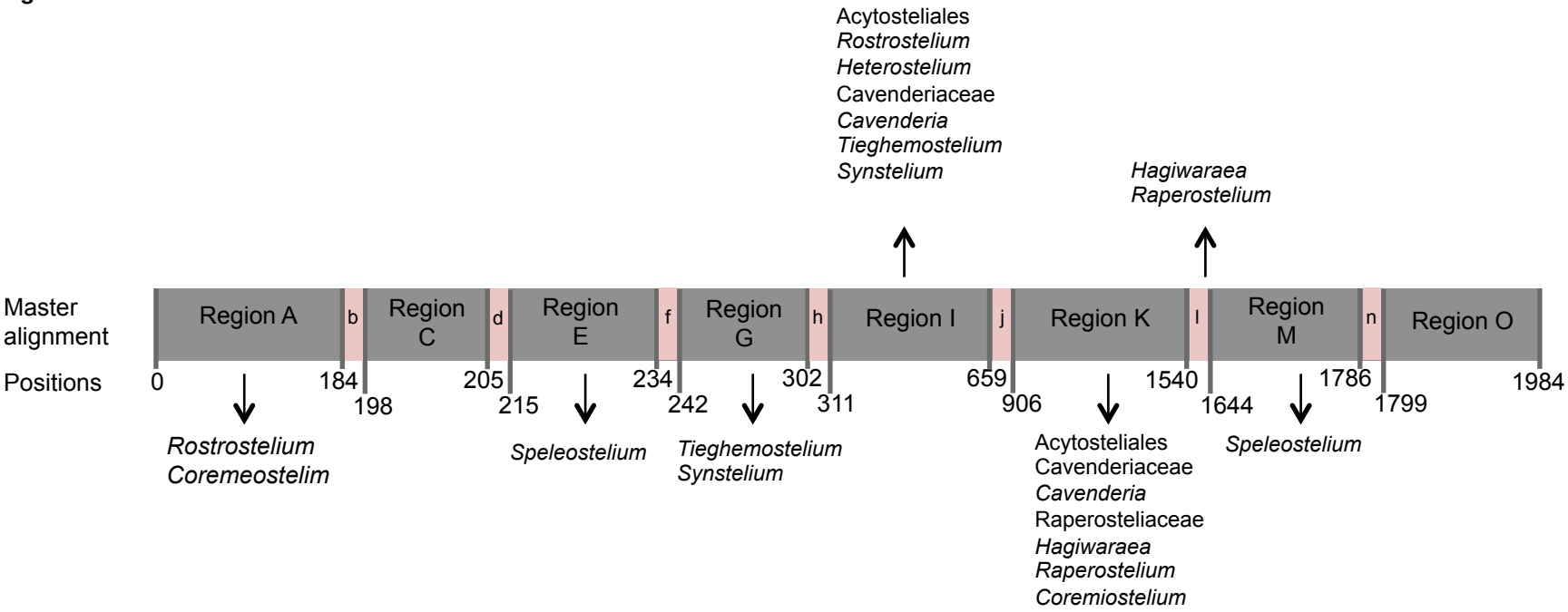
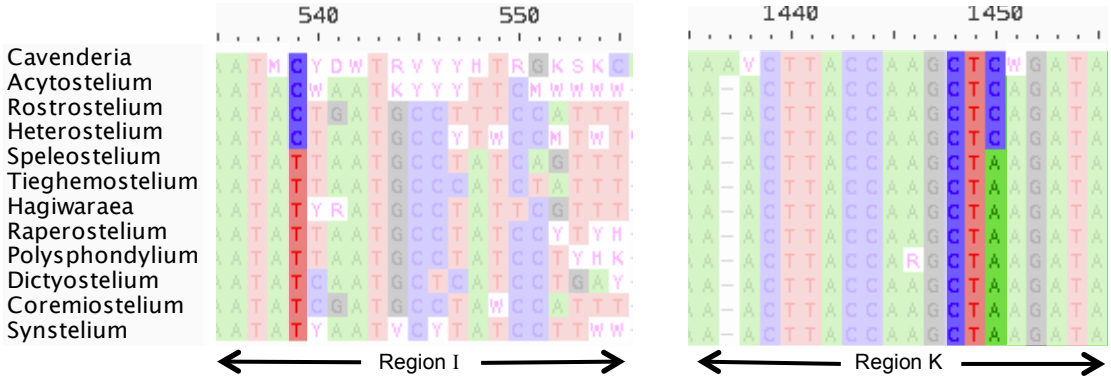
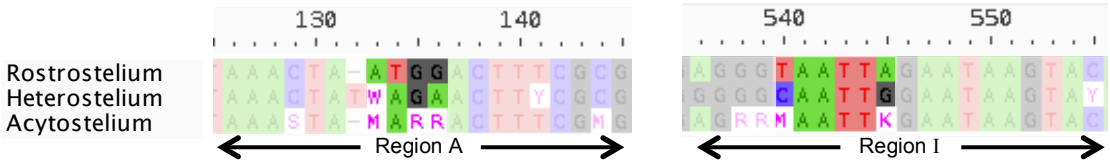

Acytosteliales
Rostrostelium
Heterostelium
Cavenderiaceae
Cavenderia
Tieghemostelium
Synstelium
Hagiwaraea
Raperostelium
Master alignment
Region A
b
Region C
d
Region E
f
Region G
h
Region I
j
Region K
l
Region M
n
Region O
Positions
0
184
198
205
215
234
242
302
311
659
906
1540
1644
1786
1799
1984
Rostrostelium
Coremeostelim
Speleostelium
Tieghemostelium
Synstelium
Acytosteliales
Cavenderiaceae
Cavenderia
Raperosteliaceae
Hagiwaraea
Raperostelium
Coremiostelium
Speleostelium

Figure3

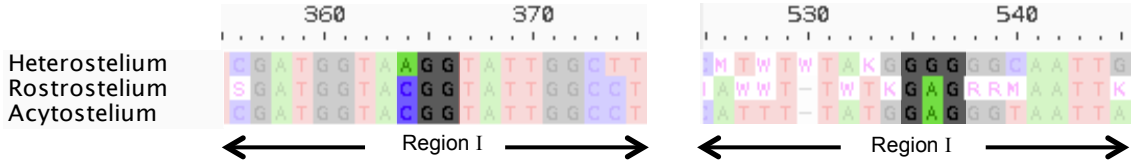
A. Acytosteliales (Supplemental material S2)



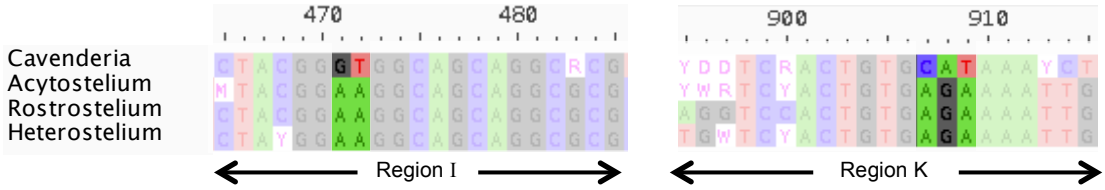
B. *Rostrostelium* (Supplemental material S3)



C. *Heterostelium* (Supplemental material S4)



D. Cavenderiaceae, *Cavenderia* (Supplemental material S5)



E. Raperosteliaceae (Supplemental material S6)

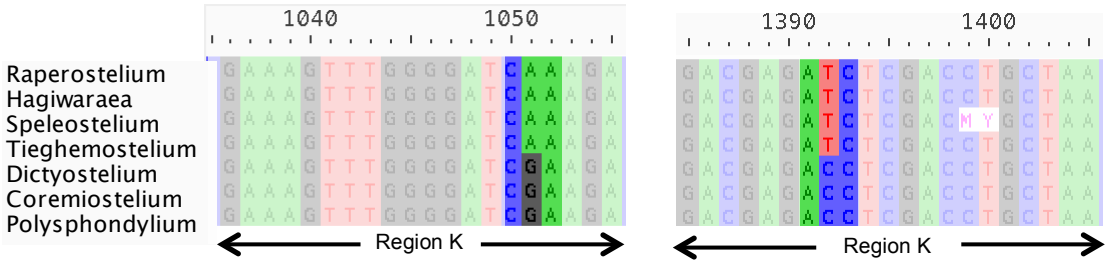


Figure4

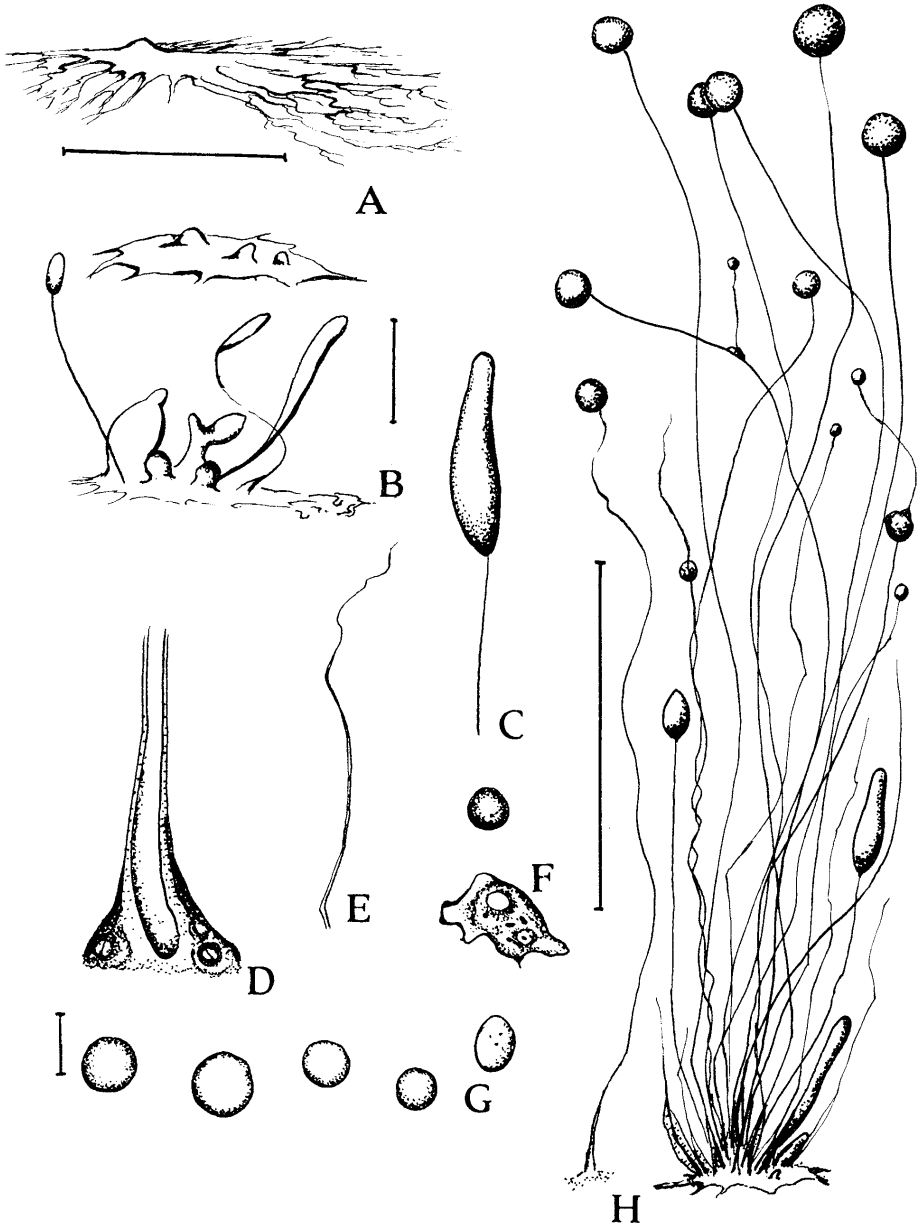


Figure5

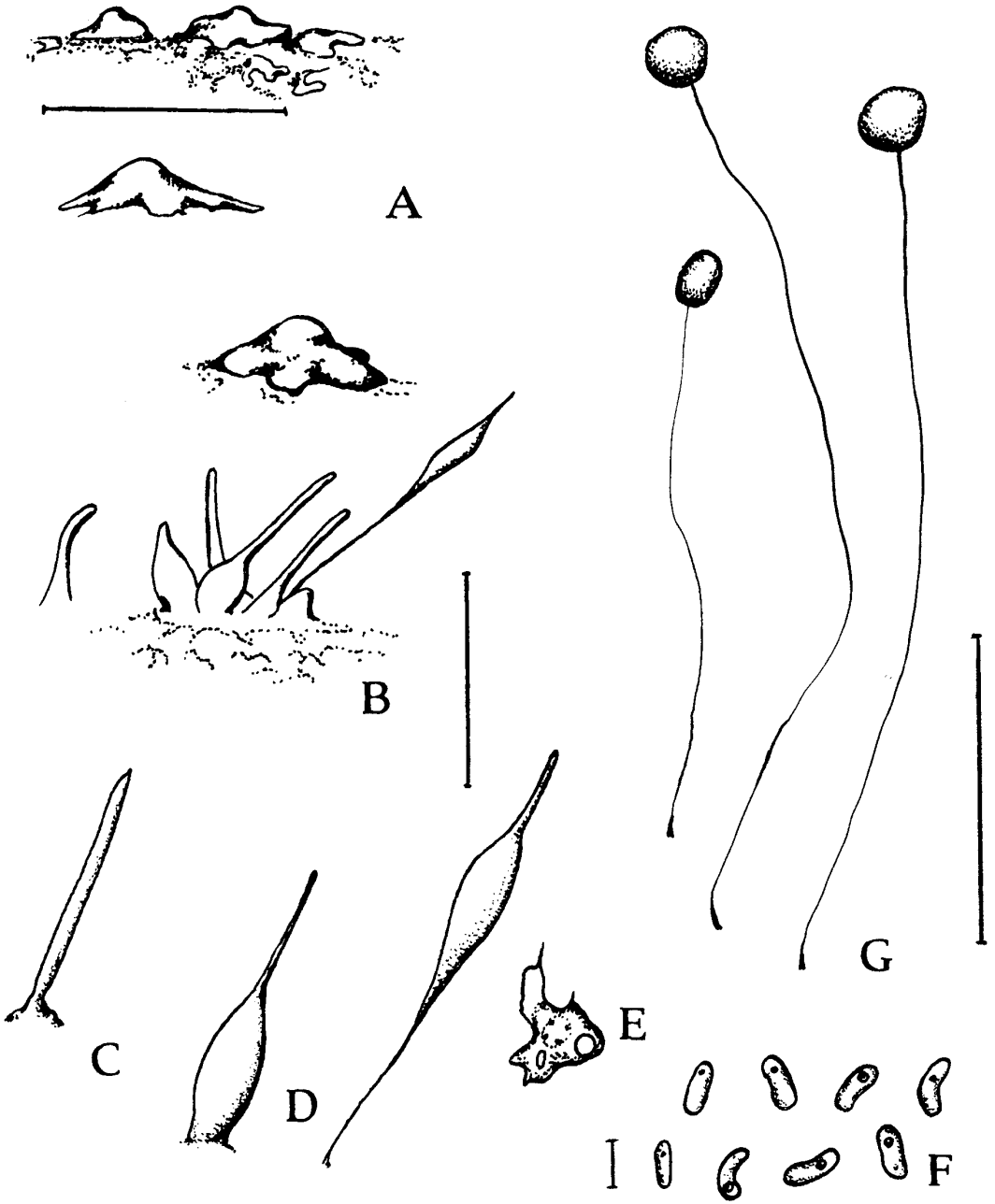


Figure6

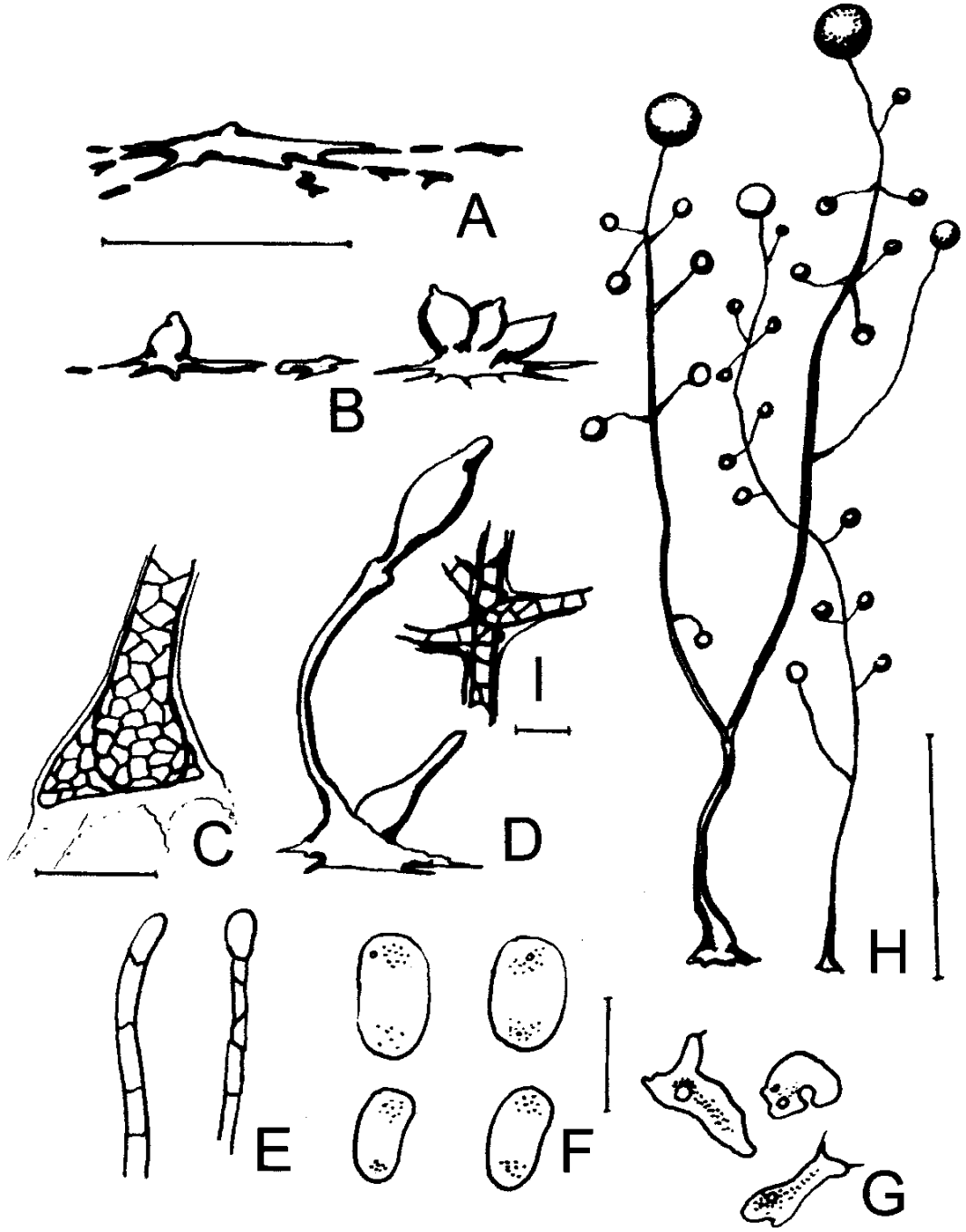


Figure7

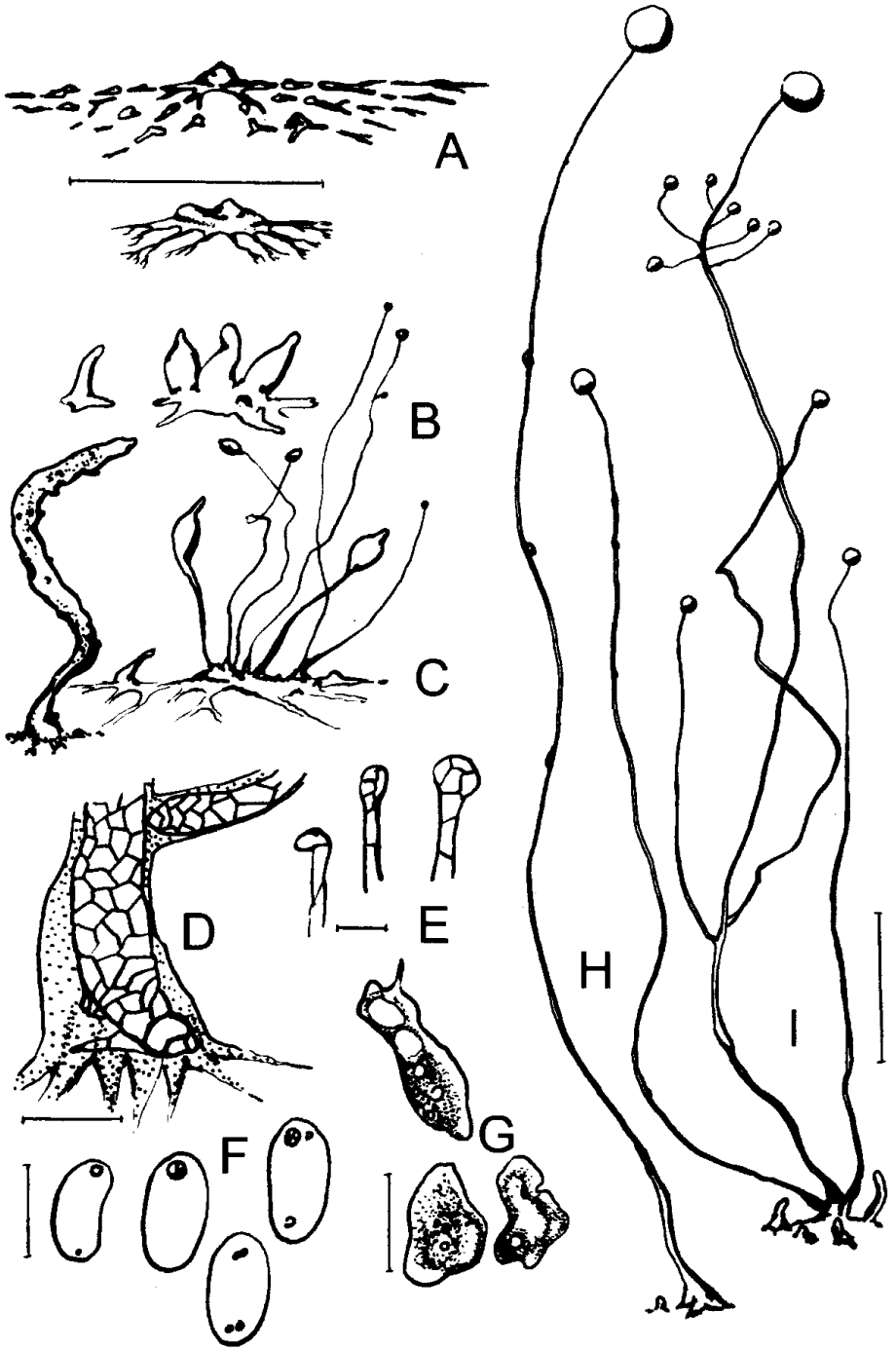


Figure8

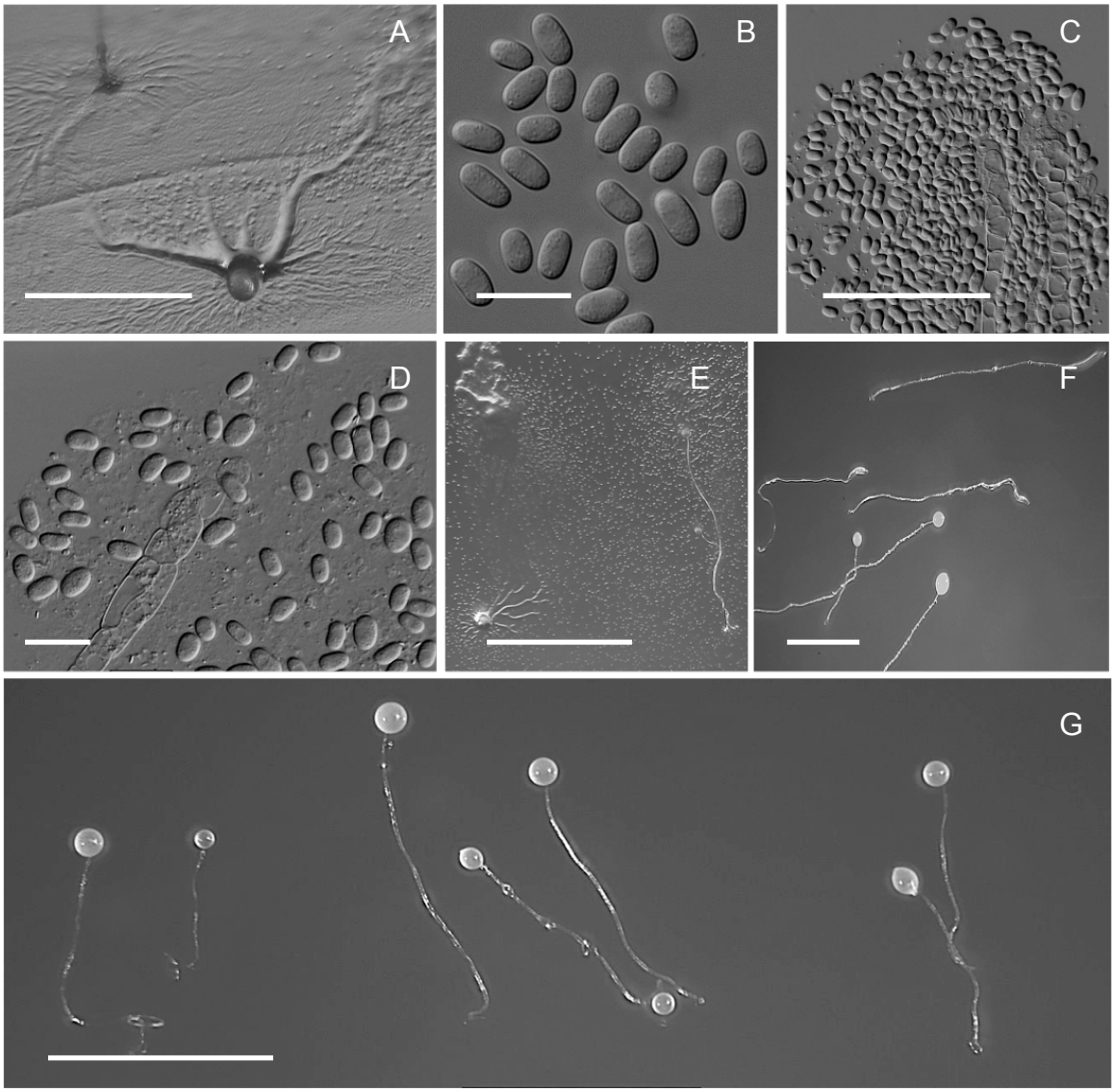


Figure9

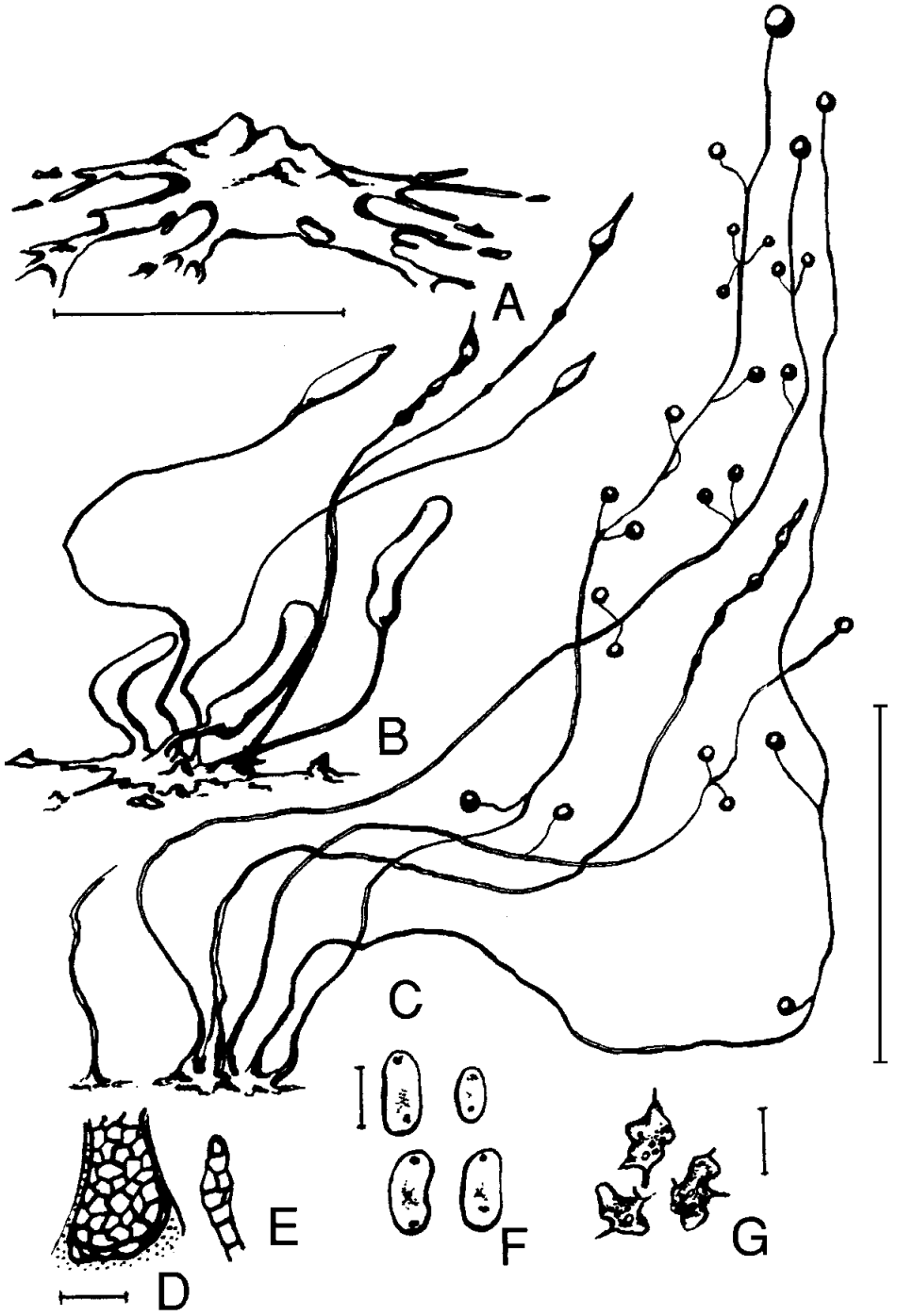


Figure10

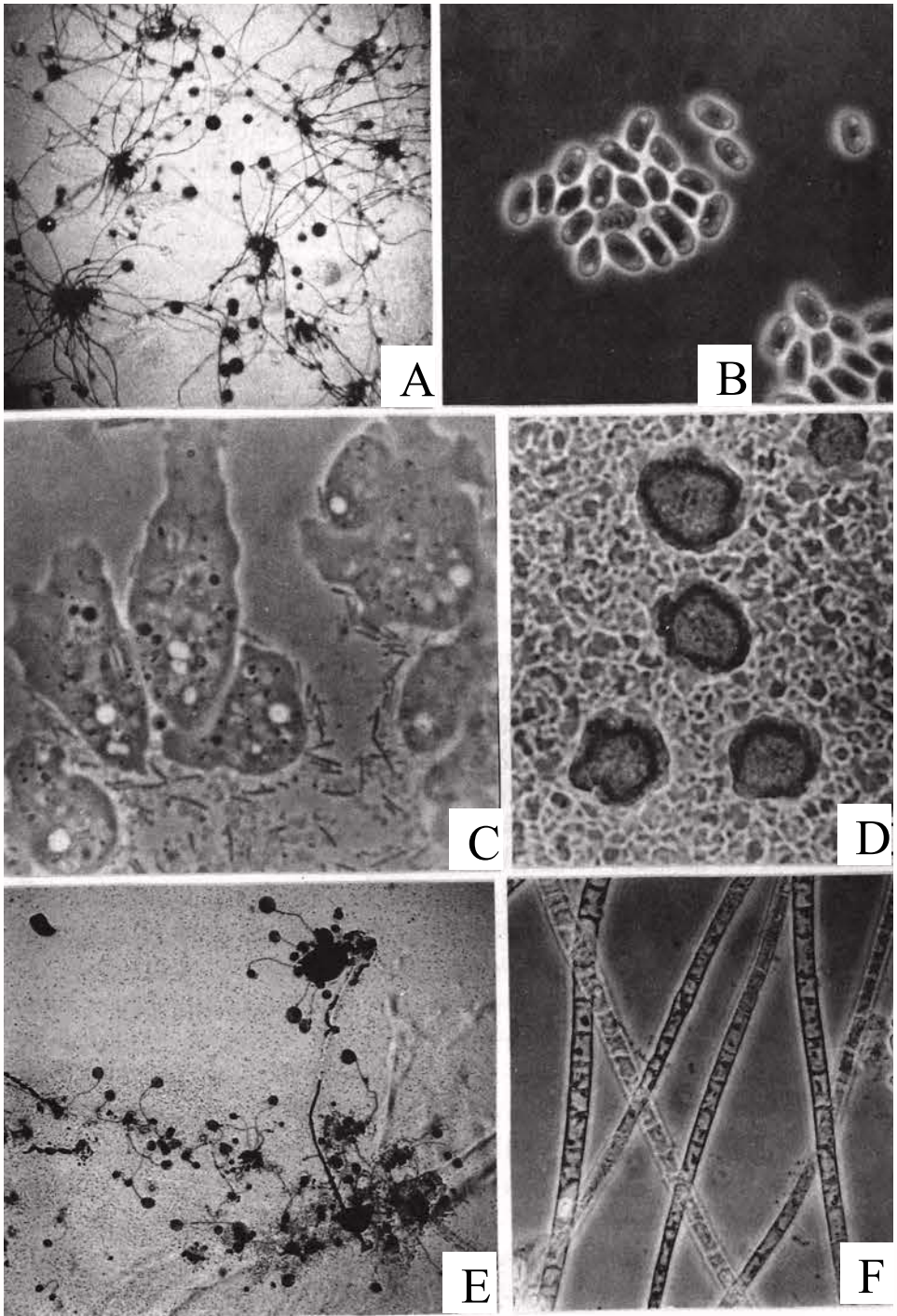
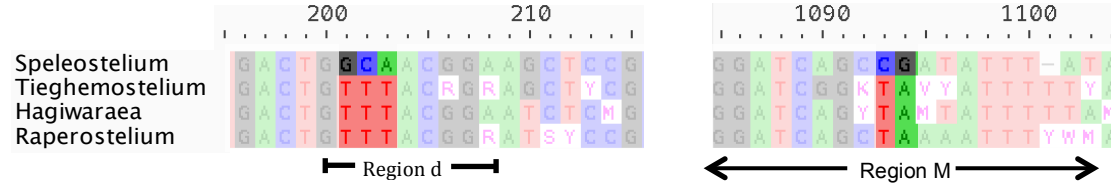
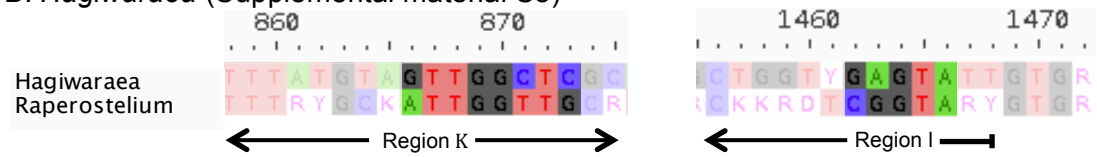


Figure11

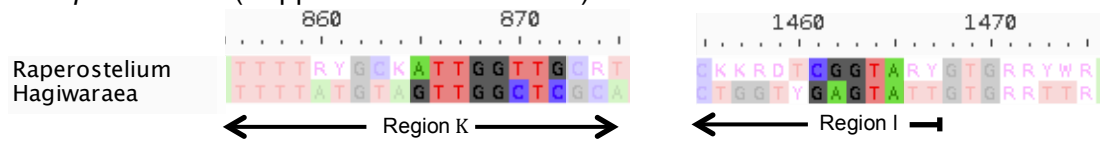
A. *Speleostelium* (Supplemental material S7)



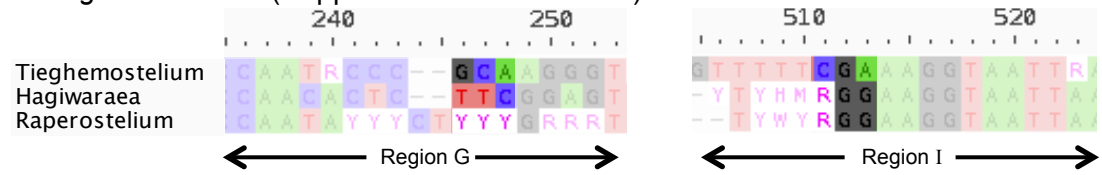
B. *Hagiwaraea* (Supplemental material S8)



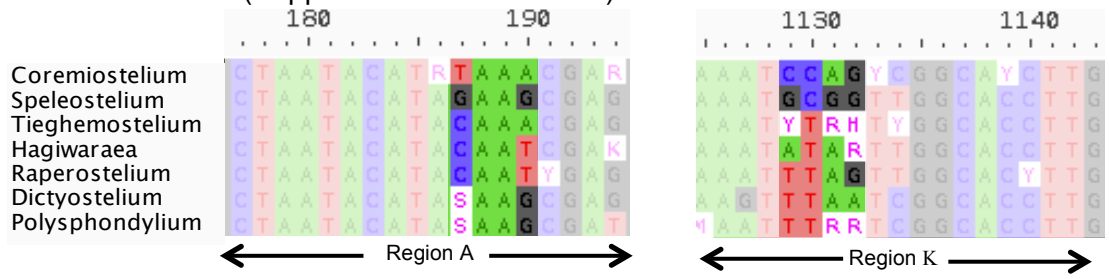
C. *Raperostelium* (Supplemental material S9)



D. *Tieghemostelium* (Supplemental material S10)



E. *Coremiostelium* (Supplemental material S11)



F. *Synstelium* (Supplemental material S12)

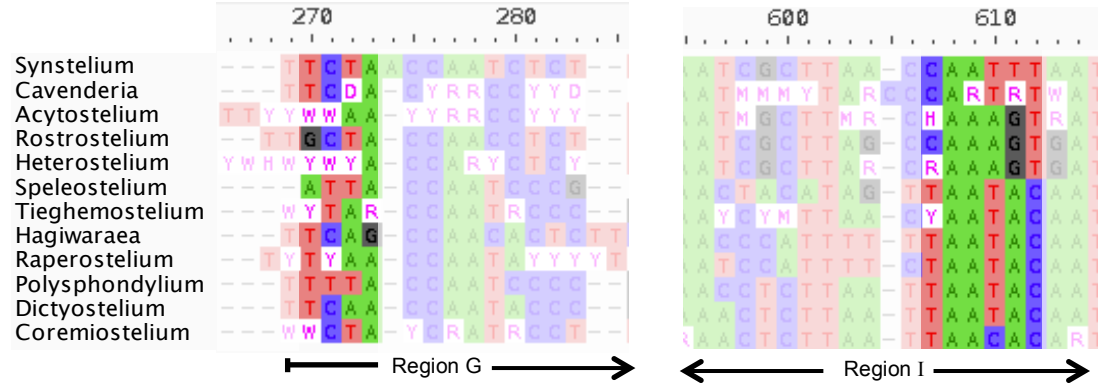


Figure12

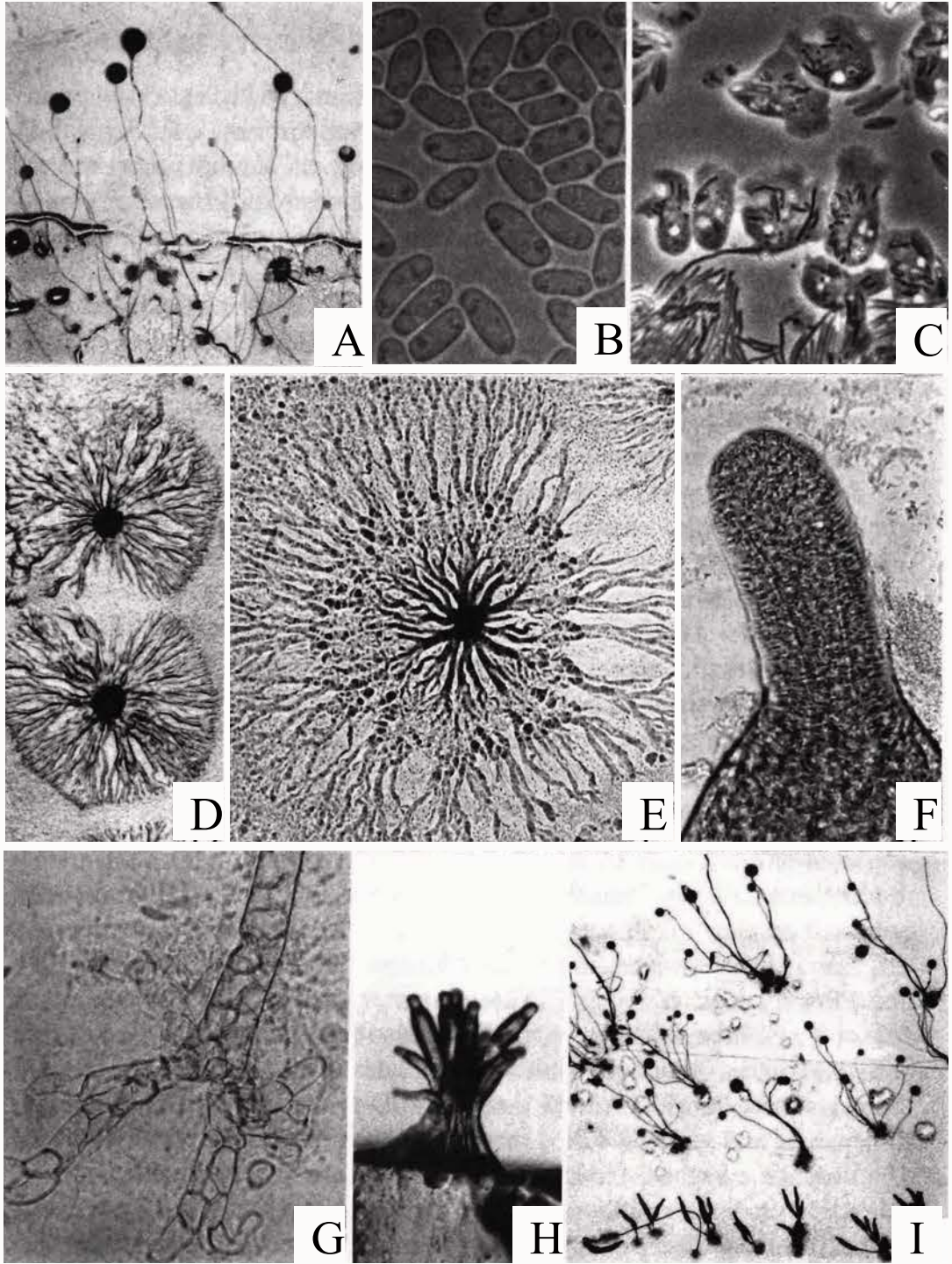


Figure13

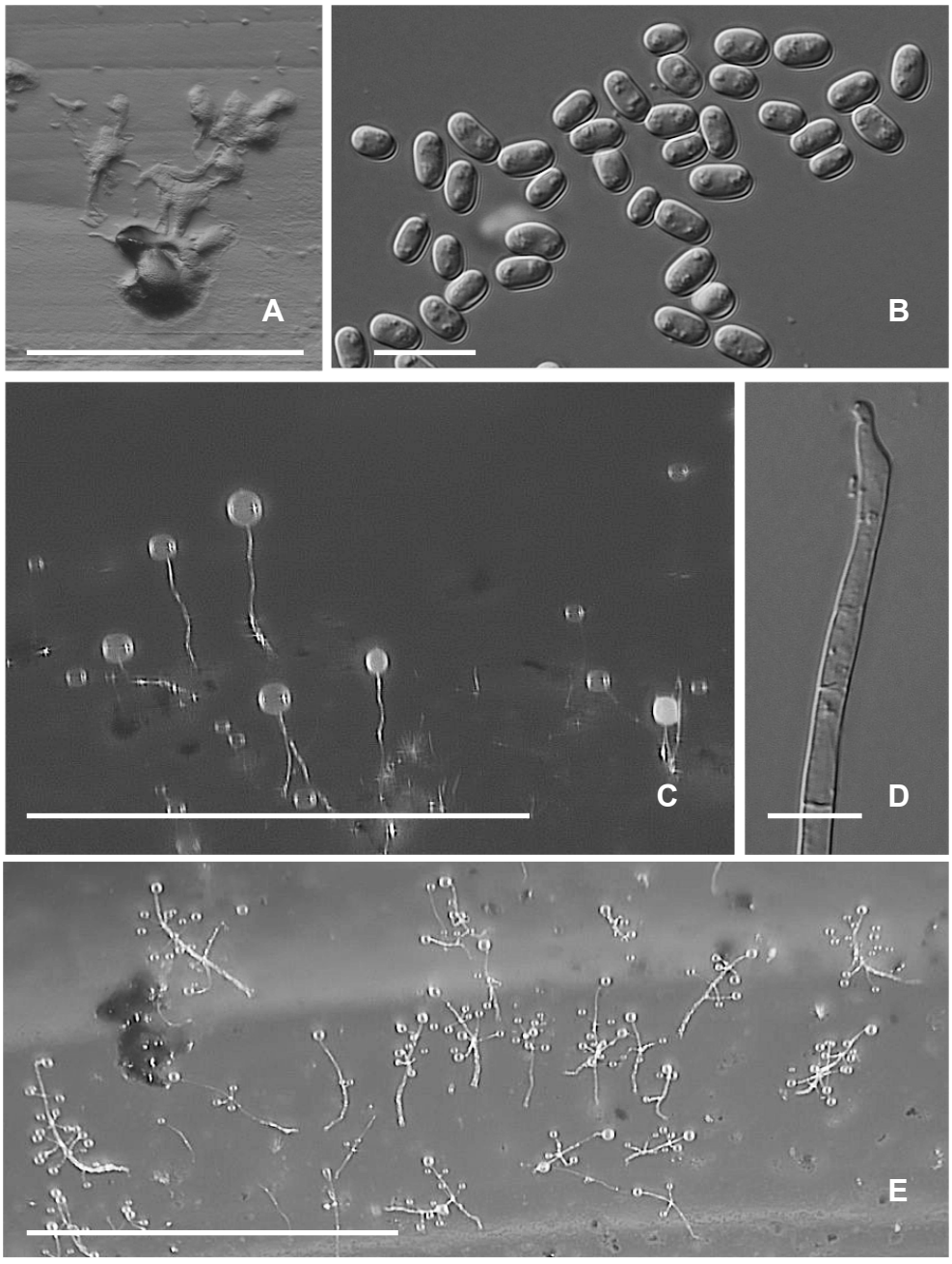


Figure14

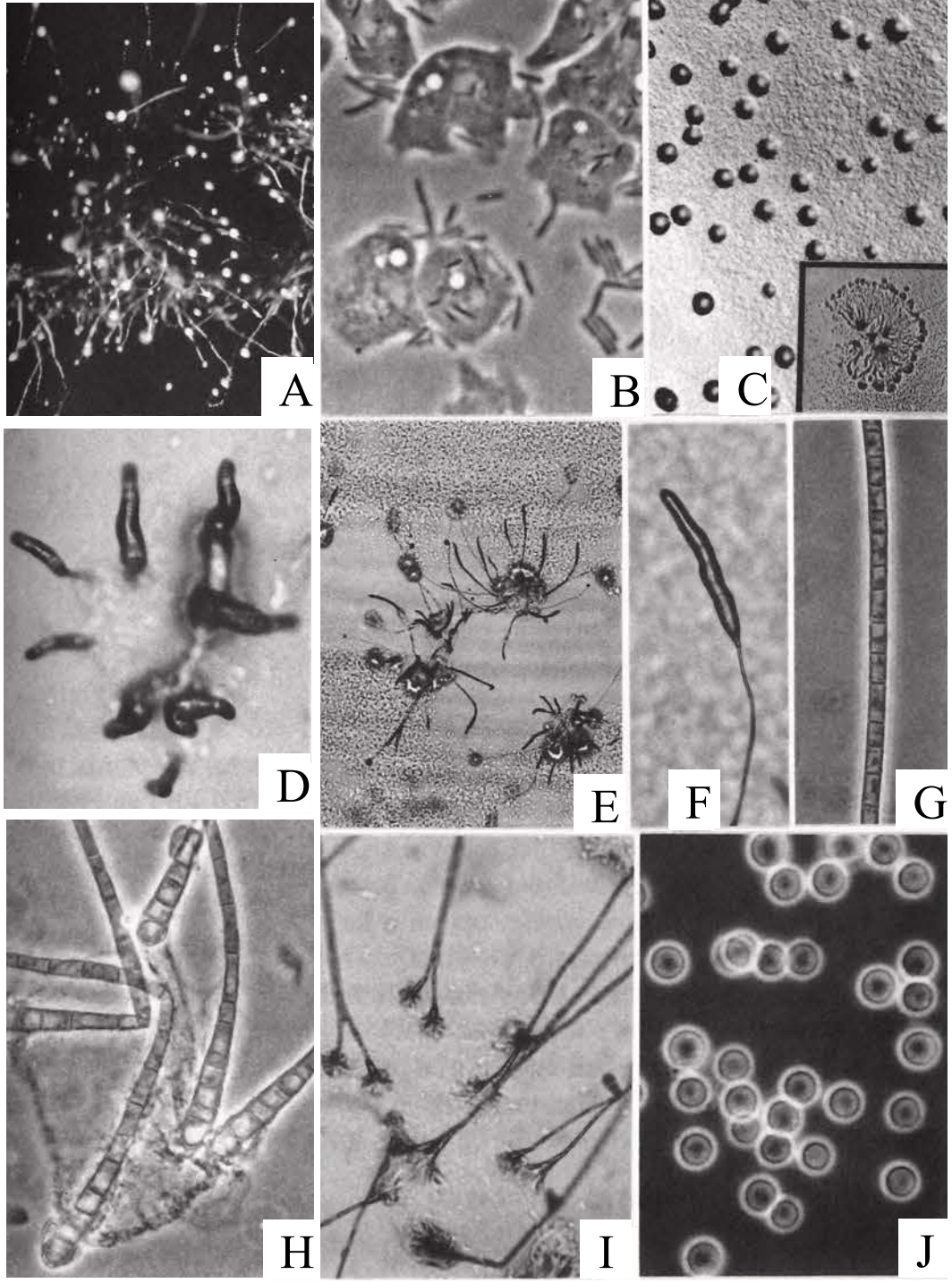


Figure15