A taxonomic summary and revision of Rozella (Cryptomycota)

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Abstract: Rozella is a genus of endoparasites of a broad range of hosts. Most species are known by their morphology and host specificity, while only three have been examined ultrastructurally and had portions of their genome sequenced. Determined in molecular phylogenies to be the earliest diverging lineage in kingdom Fungi, Rozella currently nests among an abundance of environmental sequences in phylum Cryptomycota, superphylum Opisthosphorida. Here we briefly summarize a history of Rozella, provide descriptions of all species, and include a key to the species of Rozella.

INTRODUCTION

Rozella (Cornu 1872) is a genus currently consisting of 27 species of endobiotic, holocarpic, unwalled parasites of a variety of hosts in Oomycota (Heterokontophyta), the Fungi phyla Blastocladiomycota, Monoblepharidomycota, Chytridiomycota, and Basidiomycota, and the green alga Coleochaete (Charophyta). Cornu erected the genus to describe four species, which had in common: (1) a plasmodial thallus; (2) posteriorly uniflagellate zoospores (for three of the species) that escape through a circular opening that results from the dissolution of a papilla; and (3) the formation of spherical, thick walled resting spores with spiny ornamentations. Cornu’s species were described as R. monoblepharidis polymorphae, R. rhipidii spinosi, R. apodyae brachynematis, and R. septigena; he did not hyphenate the names, but these are to be added (Art.23.1). These names were those used when the species were formally described, but Cornu (1872) interchanged long and short versions of the specific epithets in the text: monoblepharidis polymorphae and monoblepharis, rhipidi spinosi and rhipidi, and apodyae brachynematis and apodyae. Dick (2001: 246) treated the long and short versions as alternative names, and stated that “the selected epithet is therefore determined by accepted usage” and pointed out that Fischer (1892), Minden (1915), Sparrow (1938), and Karling (1942b) had used the shorter versions, and he followed their choice, rather than the longer versions used by Sparrow (1960) or Karling (1977), “because the shorter version does not imply species specificity.” We concur with this interpretation as that choice was first made in 1892, and use the shorter versions here; thus, the first three of Cornu’s species are herein subsequently referred to as R. monoblepharis, R. rhipidi, and R. apodyae.

No type species was designated. The first three species induced hypertrophy (swelling as a result of an increase in cell size) of the infected portion of the host, and each parasite thallus formed a single sporangium. The fourth-named species was distinguishable from the others by the absence (or slightness) of host hypertrophy and by the formation from the thallus of a linear series of sporangia that were separated from each other by cross walls. Thus, at conception, there were two morphologically distinct forms within Rozella, the “sporangium” (monosporangiate) form containing Cornu’s first three species, and the “septigena” (polysporangiate) form containing R. septigena. Subsequently, the developmental distinction (monosporangiate vs polysporangiate) was regarded as important, such that Fischer (1892) erected the genus Pleolpidium for the monosporangiate members of Rozella, with P. monoblepharis as the type species, and retained Rozella for the polysporangiate form, with R. septigena as the type species. Clements & Shear (1931:234) reiterated R. septigena as the type species for Rozella.

Foust (1937) discovered a second polysporangiate species, R. allomycis. Following Foust’s discovery, Sparrow (1938) stated a taxonomic issue: “The disposition of Cornu’s R. septigena and R. allomycis Foust is dependent upon how inconclusively the genus is to be interpreted. If it [Rozella] is to be restricted to those species in which a single sporangium results from an infection, then [those] two species [R. septigena and R. allomycis] would be excluded and a new genus would have to be made for their accommodation.” Sparrow (1938) and Karling (1942b) discussed in detail the taxonomic standing of Pleolpidium, and Sparrow (1938) treated Pleolpidium as a synonym of Rozella. A third polysporangiate species, R. achlyae, was discovered and described by Shanor (1942).

To accommodate the divergent morphology observed among Rozella species, Batko (1977) erected the generic name Skiriellia to accommodate the three polysporangiate species, as S. achlyae, S. allomycis, and S. septigena (the
Batko included the type of Rozella in his concept of Skirgiella, his generic name is illegitimate as it was nomenclaturally superfluous (Arts 52.1, 52.2). This also means that Doweld (2014)’s introduction of the family name Skirgiellaceae was also illegitimate as it was based on an illegitimate generic name (Art. 18.3); Doweld also validated two epithets of species first described invalidly in Rozella as they had lacked a Latin diagnosis, achlyae and allomyctis; the necessary nomenclatural corrections are provided below.

Currently, Rozella consists of 24 monosporangiate and three polysporangiate species. Held (1972a, b, 1973a, b, 1974, 1975, 1980, 1981) provided seminal insights regarding the morphology, physiology, and ultrastructure of the polysporangiate R. allomyctis, and his observations served as a basis for later comparisons among other species. Recent investigations (Letcher et al. 2017, 2018) have revealed similar zoospore morphologies among monosporangiate and polysporangiate species, indicating that regardless of thallus morphology or host specificity, zoospore ultrastructure is quite similar.

The Rozella life-cycle has been described elsewhere, so can be summarized. When viewed with light microscopy, the zoospore is elongate, 1.2–2.2 µm diam (Fig. 1A), the size difference dependent upon species. Zoospores encyst and attach to the host thallus (Fig. 1B). In polysporangiate forms, the parasite induces host hyphae to produce septa, compartmentalizing the parasite plasmodia as they develop into unwalled sporangial plasmodia (Fig. 1C) or walled resting spores (Fig. 1D). In monosporangiate forms, the parasite induces host hypertrophy (Fig. 1E). At maturity, zoospores may or may not swim in the sporangium before discharge, and may emerge as a mass and immediately disperse (Fig. 1F–I). In electron microscopy, the zoospore (Fig. 2A–C) is sphaerical to elongate, 1.2–2.2 µm diam, with a helmet-shaped nucleus (Held 1975) that is anteriorly convex and posteriorly concave, located in the anterior end of the zoospore. In the R. rhizoclosmatii zoospore, a lattice composed of perpendicular rods, as shown by serial sections (Letcher et al. 2017) is appressed to the surface of the nucleus (Fig. 2D). Posterior to the nucleus is a single sphaerical mitochondrion nestled into the concave surface of the nucleus (Fig. 2A–C). Posterior to the mitochondrion, a striated rhizoplast caps the kinetosome at the anterior end of the flagellum (Fig. 2B–C). The flagellum extends posteriorly from the kinetosome, through a cavity in the plasma membrane (Fig. 2A–C). In the central region of the zoospore is a microbody-lipid globule complex (MLC) composed of one or more lipid globules, a microbody, and a backing membrane, and ribosomes are dispersed in the cytoplasm (Fig. 2A–C).

Motile zoospores are attracted to the host, round up, and then encyst (Fig. 2E–F). In infection by R. allomyctis, intact host cytoplasm of Allomycetes is distinguishable by the presence of concentric bodies (Figs 2E, 5A, 6A). The cyst produces an appressorium that attaches to the host wall (Fig. 2E–I). An infection tube extends from the appressorium and penetrates the host cell wall (Fig. 2I). The host plasma membrane is pushed inward as the parasite protoplast is discharged through an opening in the infection tube. Empty cysts (Fig. 2E, H) eventually collapse (Fig. 2I). The parasite protoplast occupies a compartment within the host cytoplasm (Fig. 2E, G, I), then enlarges into an unwalled sporangial plasmodium (Fig. 3A) or walled resting spore (Fig. 6). In sporangial plasmodium development, the plasmodium produces lobed extensions that phagocytize host cytoplasm (Figs 3B, 4A); often a vacuole occupies the center of the plasmodium (Figs 3B, 4A). At maturity the multinucleate sporangial plasmodium (Figs 3B, 4A) becomes a zoosporangium that completely fills the host (Fig. 4B). Numerous zoospores are cleaved (Figs 4B, 5) and released through a discharge pore (Fig. 5B) or tube (Fig. 5C). In resting spore development, multiple plasmodia occupy a host compartment (Fig. 6A). Resting spore plasmodia are irregular in outline at first, but eventually become sphaerical (Fig. 6A), and resting spores of most Rozella species have spiny wall ornamentation (Fig. 6B).

Rozella has engendered much interest over the last decade, beginning with two strains in a molecular phylogeny that occurred as the earliest diverging lineage in the fungi (James et al. 2006). One strain (JEL 347, R. rhizoclosmatii) was monosporangiate, while the second (UCB 47-54, R. allomyctis) was polysporangiate. Subsequently, this lineage came to include not only the two strains of Rozella, but a myriad of novel small subunit ribosomal RNA gene sequences (SSU rRNA) derived from environmental surveys (e.g. Lara et al. 2010, Jones et al. 2011a, Karpov et al. 2014, Lazarus & James 2015, Grossart et al. 2016, Rojas-Jimenez et al. 2017, Tedersoo et al. 2017). Initially referred to as the Rozella clade (James et al. 2006), then “Rozellida” (Lara et al. 2010), the lineage is now assigned to the Cryptomycota (Jones et al. 2011b), and more recently has been also referred to as Rozellomyctota (e.g. Corsaro et al. 2014) and Rozellosporidida (Karpov et al. 2017). Because of the position of Cryptomycota in expanded molecular phylogenies, different schools of thought exist as to its actual affinity. James et al. (2013) proposed that Cryptomycota and Microsporidia share a common ancestor. Karpov et al. (2014) erected the superphylum Opisthosporidio to include three phyla: Cryptomycota, Aphelida, and Microsporidia. Cryptomycota was considered sister to Fungi. More recently, Tedersoo et al. (2017) placed Aphelida as sister of Blastocladiomycota in kingdom Fungi, and Cryptomycota + Microsporidia as a lineage sister to Fungi. Bass et al. (2018), however, placed Cryptomycota as sister to Microsporidia. In this taxonomic summary we use the most current hierarchical taxonomic framework (Tedersoo et al. 2018). Obviously, much work remains to confirm the placement of Rozella and Cryptomycota.

There has been considerable confusion over names to be applied to these organisms, and here we aim to provide a comprehensive summary of the taxonomy and nomenclature of both the phylum and the genus Rozella based on the current International Code of Nomenclature for algae, fungi and plants (ICN; Turland et al. 2018).
Taxonomy of Rozella (Cryptomycota)

The following taxonomic summary is based on our understanding and interpretation of these organisms. Additionally, without morphological, molecular, or ultrastructural evidence to the contrary, we include holocarpic, posteriorly uniflagellate Rozella species that previously have been excluded from the genus (Dick 2001).

SUPERGROUP: Opisthokonta Cavalier-Smith, in Rayner et al., Evol. Biol. Fungi: 344 (1987).

Circumscription emended by Cavalier-Smith & Chao (1995) and Adl et al. (2005).

SUPERKINGDOM: Holomycota Y. Liu, BMC Evol. Biol. 9:272: 3 (2009).

SYNONYM: Nucleomycetia M.W. Brown, Mol. Biol. Evol., 26: 2706 (2009).

KINGDOM: Fungi R.T. Moore, Bot. Marina 23: 371 (1980).

SUBKINGDOM: Rozellomyceta Tedersoo et al., Fungal Divers.: doi.org/10.1007/s13225-018-0401-0: 13 (2018).

Fig. 1. Light microscopic images of Rozella. A. Motile zoospore of R. rhizoclosmatii [strain JEL 863, Letcher et al. 2017]. B–D. R. allomycetis and its host Allomyces macrogyrus [strain UM690, unpubl.]. B. Encysted zoospores on host hypha. C. Parasite sporangia in septate segments of host hypha. D. Spiny parasite resting spores in septate segments of host hypha. E. Rozella rhizoclosmatii. Uninfected sporangium of host Rhizoclosmatium globosum, with discharged zoospores (arrow); infected, hypertrophied host sporangia (arrowheads) [strain JEL 863, Letcher et al. 2017]. F–I. Rozella multimorpha. Zoospore release from terminal sporangium in infected host Pythium catenulatum [strain JEL 883, unpublished; see Letcher et al. 2018]. Abbreviations: CB, concentric bodies; H, host; PSp, parasite sporangium; PRS, parasite resting spore; Sep, septum. Bars A = 1 µm, B–D = 15 µm, E = 100 µm, F–I = 10 µm.
Fig. 2. Transmission electron microscopic images of Rozella zoospores and infection. A. *R. allomycetis* [strain CSF 55; Powell et al. 2017]. B. *R. multimorpha* [strain JEL 883; Letcher et al. 2018]. C–D. *R. rhizoclosmatii* [strain JEL 863; Letcher et al. 2017]. D. A lattice of perpendicular rods (arrows) about the nucleus. E–I. *R. allomycetis* [strain UM 690; Powell and Letcher, unpubl.] parasitizing *Allomyces macrogynus*. E. Early stages of infection. F. Encysted zoospore. G. Zoospore cyst and early infection. H. Empty zoospore cyst. I. Collapsed zoospore cyst and early parasite protoplast. Abbreviations: A, appressorium; C, zoospore cyst; Cav, posterior cavity; CB, concentric body; CC, collapsed zoospore cyst; EC, empty zoospore cyst; F, flagellum; H, host; IT, infection tube; K, kinetosome; L, lipid globule; M, mitochondrion; N, nucleus; P, parasite; Rh, rhizoplast; Z, zoospore. Bars A, F–I = 0.5 μm, B–D = 0.25 μm, E = 2 μm.
Taxonomy of Rozella (Cryptomycota)

Diagnosis: “Vegetative cells amoeboid, with pseudopodial extensions extending around host organelles; zoospores with a posterior flagellum that has a solid rhizoplast associated with a long kinetosome; one single large mitochondrion (missing in Microsporidea); resting spores thick-walled; chitinous wall present only in some life stages; penetration of host cells via germ tube; intracellular obligate parasites of fungi, animals and protists that consume host organelles via phagocytosis” (Tedersoo et al. 2018).

Type: Rozella Cornu 1872.

Superphylum: Opisthosphoridia Karpov et al., Frontiers Microbiol. 5: 8 (2014).

Phylum: Cryptomycota M.D.M. Jones & T.A. Richards, MycoBank MB827617

Basionym: Skirgiellia achlyae Doweld, Index Fung. 129: 1 (2014).

Synonyms: Rozella achlyae Shanon, J. Elisha Mitchell Sci. Soc. 58: 100 (1942); nom. inval. (Arts. 39.1, 40.1).

Description: “An endotrophic parasite of Achlya flagellata causing very slight or no hypertrophy. Young plasmodium hardly distinguishable in the host protoplasm, hyaline and very nearly optically homogeneous. Sporangial formed in a linear sori, cylindrical to somewhat barrel shaped, length and width depending largely upon that of host hyphae; exit papillae short, about 1.5 µm in length, rupturing following gelatinization of the tips. Zoospores swimming in a jerky and darting manner, ovoid, 2–3 × 3–4 µm with a single refractive globule, single flagellum posteriorly attached, usually 12–15 µm in length. Resting bodies produced in segments formed in host hyphae that resemble sporangial sori, each segment containing from one to many resting bodies. Resting bodies spherical to oval, 12–6–23.7 µm in diameter (not including spines), mostly 15.8–17.3 µm, usually covered with fine tenuous spines which commonly measure about 1.6–2.3 µm in length, wall of mature resting bodies thick, reddish-brown to amber brown in color. Resting spore gelatinization follows a dormant period and is accomplished by the formation of posteriorly unflagellate zoospores which escape through an exit papilla” (Shanor 1942).

Hosts: Achlya flagellata, A. proliferoides, Dictyuchus anomalous, and D. monosporus (Johnson 1955) (Oomycota).

Rozella allomycetis (Doweld) Letcher, comb. nov.

MycoBank MB827616

Basionym: Skirgiellia allomycetis Doweld, Index Fung. 129: 1 (2014); as “allomycis”.

Synonym: Rozella allomycis Foust, J. Elisha Mitchell Sci. Soc. 53: 198 (1937); nom. inval. (Arts. 39.1, 40.1).

Description: “Fungus body parasitic within the distal parts of the hyphae of Allomyces. Sporangial first formed at the tips of the young host hyphae, usually 1–5 in a row, in basipetal succession; usually barrel-shaped, but varying greatly in size

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**Fig. 3.** Plasmodial development in *Rozella*. A. Early plasmodial formation of *R. multimorpha* [strain JEL 883; Letcher *et al*. 2018] in host *Pythium catenulatum*. B. Multinucleate plasmodium of *R. allomycetis* [strain CSF 55; Powell *et al*. 2017] in host *Allomyces arbuscula*; plasmodium has a central vacuole. Abbreviations: H, host; P, parasite plasmodium; PN, parasite nucleus; Vac, vacuole. Bars = 5 µm.

**Fig. 4.** Plasmodial development in *Rozella*. A. Multinucleate plasmodium of *R. rhizoclosmatii* [strain JEL 863; Letcher *et al*. 2017] in host *Rhizoclosmatium globosum*; plasmodium has a central vacuole. B. Early zoospore cleavage of *R. allomycetis* [strain CSF 55; Powell *et al*. 2017] in host *Allomyces arbuscula*; nuclei and mitochondria are organized and flagella appear in cleavage furrows. Abbreviations: F, flagella; PM, parasite mitochondrion; PN, parasite nucleus; Vac, vacuole. Bars = 1 µm.
Taxonomy of Rozella (Cryptomycota)
and shape, 12–20 × 20–40 μm, more often about 15.9 μm × 24.6 μm. The wall apparently confined to the original host wall. Usually with one exit papilla, which is about 1.3 μm long. Frequently a primary sporangium may be divided by one or more partitions into several smaller sporangia. Zoospores ovoid, the posterior end the larger, about 3–4 μm thick, containing one refractive globule and with one posteriorly attached flagellum, which is four times the length of the spore and is directed backward when the spore swims. Swimming by darting about with frequent changes of direction as typical for chytrid spores. The swimming period lasting about an hour, after which the spores germinate or die. Resting bodies formed later than the sporangia, occurring in the distal part of the host hyphae just behind the sporangia in swollen segments that are 1–35 in number, each segment containing from 1–16 resting bodies, the average being about 3 or 4. Segments spherical, barrel-shaped, nearly cylindrical, or irregular, 20–40 × 20–70 μm. Segments not completely filled by resting bodies, usually containing some left-over, dead, granular, host protoplasm. Resting bodies with spiny walls, spherical, 12–20 μm thick, averaging about 15.9 μm thick (average of 20 measurements) counting the spines which are about 1.3 μm long; yellowish brown to reddish brown in color; when mature with a thick (.5 μm) wall, with a central

Fig. 5. Completed zoospore formation in Rozella. A. Zoospores of *R. allomycetis* [strain CSF 55; Powell et al. 2017] in host *Allomyces arbuscula*; septum separating host from parasite was induced by parasite. B. Zoospores of *R. allomycetis* [strain CSF 55] being released through a discharge pore. C. Zoospores of *R. multimorpha* [strain JEL 883; Letcher et al. 2018] in host *Pythium catenulatum*; some spores are in the discharge tube. Abbreviations: CB, concentric body; DP, discharge pore; DT, discharge tube; FP, flagellar pool; H, host; P, parasite; S, septum; Sp, sporangium; Z, zoospore. Bars = 5 μm.
hyaline globose mass of material surrounded by a granular zone of protoplasm. Germinating after a rest period of a week to form zoospores if fresh water is added and a young culture of Allomyces is present. The resting bodies may retain their vitality either dry or wet for several weeks, perhaps months. Zoospores from resting bodies identical with those from regular sporangia and capable of infecting young host hyphae” (Foust 1937).

Hosts: Allomyces arbuscula, A. javanicus, A. macrogynus, and A. anomalus (Blastocladiomycota).

Notes: Ultrastructure of the host-parasite interface between R. allomycetis and Allomyces anomalus has been studied (Powell et al. 2017), as has been ultrastructure of early infection stages of R. allomycetis in A. macrogyrus (Powell & Letcher, unpubl.). Foust’s epithet “allomycis” was corrected to “allomycetis” by Doweld (2014), as the correct genitive case of the host genus Allomyces. Sparrow (1960) noted that Rozella allomycetes was “A name unaccompanied by a description. Probably referable to Rozella allomycis Foust”.

Rozella apodyae Cornu, Ann. Sci. Nat., Bot., sér. 5, 15: 161 (1872).

Synonyms: Rozella apodyae-brachynematis Cornu, Ann. Sci. Nat., Bot., sér. 5, 15: 161 (1872).

Rozella apodachlyae M.W. Dick, Stramin. Fungi: 373 (2001); as “M. Cornu”; nom. illegit. (Art. 52.1).

Pleolpidium apodyae-brachynematis (Cornu) A. Fischer, Rabenh. Krypt.-Fl. 1 (4): 45 (1892); as “apodyae”.

Type: Cornu (Ann. Sci. Nat., Bot., sér. 5, 15: pl. 5, figs 10–14, 1872; lectotype designated by Dick 2001: 373).

Description: “Sporangium filling the sporangium of the host and assuming its shape, with a small apical papilla; zoospores somewhat elongate, with a posterior flagellum, escaping through a small pore resulting from the dissolution of the papilla; resting spore formed in the sporangium of the host, spherical, somewhat thick-walled, brownish (?) covered with very short tenuous spines” (Sparrow 1960).

Host: Apodachlya brachynema (Oomyctota).
Rozella blastocladiæ (Minden) Sparrow, *Mycologia* 30: 377 (1938).

*Basionym:* *Pleopodium blastocladiæ* Minden, *Krypt. Fl. Mark Brandenb.* 5 (3): 253 (1911) [*1915*].

Type: Petersen (*Bot. Tidsskrift* 29 (4): 424, fig. 26c–d, 1909; neotype (as "lectotype") designated by Dick 2001: 374).

Description: “Sporangium assuming the shape of the hypertrophied host sporangium, which becomes somewhat broader and more ovoid than normal, with an apical pore, collapsing after discharge of the zoospores; zoospores not observed; resting spore exactly spherical, brown, thick-walled, the exospore densely covered with tenuose spines, germination not observed” (Sparrow 1960).

Hosts: *Blastocladiæ pringsheimii,* and *B. gracilis* (*Blastocladidiozymycota*).

Rozella canterae Sparrow, *Aquatic Phycom.* 2nd edn: 172 (1960).

Type: Canter (*Trans. Brit. Mycol. Soc.* 33: 357, fig. 3g–n; pl. 29, figs 4–5, 1950; lectotype designated by Dick 2001: 375).

Description: “Sporangium assuming the shape of the un hypertrophied host sporangium and completely filling it; zoospores ovoid, with a small refractive anterior globule and posterior flagellum, escaping after the operculum of the host is dehisced; resting spore somewhat ovoid, with a thick wall, the outer wall of which bears hexagonal ridges and spines” (Canter 1950, Sparrow 1960).

Host: *Chytridiomycota*.

Rozella chytriomycetis Karling, *Mycologia* 38: 107 (1946); as “chytriomycetis”.

Type: Karling (*Mycologia* 38: 104, figs 9–19, 1946; lectotype designated by Dick 2001: 375).

Description: “Sporangia solitary, hyaline, filling host cell and conforming with the latter in size and shape, usually spherical, 10–40 µm, with one to three exit papillae… zoospores hyaline, oblong or slightly clavate, 3 µm × 1.5 µm, with a minute, 0.5–0.7 µm refractive globule; swirling in sporangium before emerging; darting about rapidly in swimming, rarely becoming amoeboïd. Resting spores partly or completely filling host cell, oval or spherical, 7–20 µm, with large central vacuole, usually coarsely granular cytoplasm; wall dark brown, rarely smooth, usually spiny or echinulate; germination unknown” (Karling 1946).

Host: *Chytromyces hyalinus* (*Chytriomycota*).

Rozella cladochytrii Karling, *Torreya* 41: 105 (1941).

Type: Karling (*Amer. J. Bot.* 29: 26, figs. 1–24, 1942; *lectotype designated here,* MBT 384206).

Description: “Sporangia solitary in host cell, spherical, 10–40 µm, ovoid, ellipsoid, 10–15 µm × 15–35 µm, pyriform, and obclavate, hyaline and smooth with one to three exit papillae; zoospores obclavate, 3.3–5 µm × 1.8–2 µm, aguttulate; flagellum 14 µm long; emerging fully formed in a stream from the exit papillae and becoming actively motile in a few seconds. Resting spore faintly yellow, oval, spherical, 8–22 µm, with a large central vacuole and coarsely granular cytoplasm; wall 1–1.8 µm thick, smooth or spiny, spines 1.5–3 µm long; transformed directly into a zoosporangium in germination and forming zoospores” (Karling 1942a).

Hosts: *Nowakowskiiella profusum,* *N. elegans,* *N. ramosum,* *Cladochytrium replicatum,* *C. crassum,* and *C. hyalinum* (*Chytriomycota*).

Note: The original description (Karling 1941) lacked illustrations, thus the species is neotypified by illustrations from a later work (Karling 1942) by the same author.

Rozella coleochaetæs Sparrow, *Papers Mich. Acad. Sci. Arts Letters* 50: 118 (1965); as “coleochaetæs”.

Synonym: *Plasmophagus coleochaetæs* (Sparrow) M.W. Dick, *Straminip. Fungi* 451 (2001).

Type: Sparrow (*Papers Mich. Acad. Sci. Arts Letters* 50: 116, figs A–E, 1965; *lectotype completely designated here,* MBT 384207).

Description: “Sporangium completely filling the greatly enlarged host cell, spherical, 35–38 µm, subspherical, 40–42 × 33–40 µm, or clavate, 55 × 15–25 µm, with a single strongly protruding discharge papilla 10 µm in diameter. Zoospores numerous, 6–7 × 2–2.5 µm, fusiform, with a minute globule, motile within the sporangium, escaping through a sessile pore upon deliquescence of the papilla. Resting spore not observed” (Sparrow et al. 1965).

Host: *Coleochaete* (*Charophyta*).

Note: Blackwell et al. (2016) justified the exclusion of *R. coleochaetæs* from the genus *Plasmophagus*.

Rozella cuculus (E. J. Butler) Sparrow, *Mycologia* 30: 377 (1938).

*Basionym:* *Pleopodium cuculus* E. J. Butler, *Mem. Dept. Agric. India, Bot. Ser.* 1: 125 (1907).

Type: Butler (*Mem. Dept. Agric. India, Bot. Ser.* 1: plate VII, figs 22–25, 1907; lectotype designated by Dick 2001: 374).

Description: “Sporangium spherical, sub spherical, or pyriform, formed in the sporangium of the host or in pronounced intercalary swellings of the hyphae, 19.2–24 µm in diameter, with a single papilla; zoospores obclavate, clavate, or ovoid, the flagellum emerging from the broader end; resting spore spherical, single, free in the sporangium or intercalary swelling of the host, 12–18 µm in diameter, with a smooth pale-yellow somewhat thickened wall, germination not observed” (Sparrow 1960).
Hosts: *Pythium intermedium*, and *P. monospermum* (*Oomycota*).

Note: Sparrow (1960) putatively included *Pleopodium tuberculorum* Vuillemin (1909) and *Chytridium simulans* Dangeard (1896-97) as referable to *R. cuculus*.

*Rozella diplophyctidis* Karling, *Nova Hedwiga* 45: 529 (1987).

Type: Karling (*Nova Hedwiga* 45: 534, figs 1–6, 1987 – holotype).

Description: “Sporangia filling the host sporangia, spherical to subspherical, 18–28 µm diameter, ... and 1–4 exit papillae. Zoosporos ovoid to slightly elongate, 1.8–2.5 µm diameter, with a small hyaline refractive globule. Resting spores partly filling host cell, spherical, 16–22 µm, with a brown spiny wall. Germination unknown” (Karling 1987).

Host: *Diplophysctis intestina* (*Chytridiomycota*).

*Rozella endochytrii* Karling, *Torreya* 41: 106 (1941).

Type: Karling (*Amer. J. Bot.* 29: 30, figs 25–35, 1942; *neotype designated here*, MBT 384208).

Description: “Sporangia solitary in a host cell, spherical, 15–200 µm, oval, elongate, pyriform and irregular, depending on the size and shape of the host cell; wall of the sporangium hyaline and smooth with one to several exit papillae, 2–6 µm high. Zoosporos ovoidoblate, 3.4–4 µm × 1.5 µm, aguttulate but with optically denser apical and basal regions which give them a characteristic appearance; swirling in the sporangium before dehiscence; emerging in a stream and becoming actively motile in a few seconds. Resting spores unknown” (Karling 1942a).

Host: *Endochytrium operculatum* (*Chytridiomycota*).

Note: The original description (Karling 1941) lacked illustrations, so the species is lectotyped by illustrations from a later work (Karling 1942) by the same author, of the original material.

*Rozella irregularis* (E. J. Butler) Sparrow, *Myologia* 30: 377 (1938).

Synonym: *Pleopodium irregulare* E. J. Butler, *Mem. Dept. Agric. India, Bot. Ser.* 1: 123 (1907).

Type: Butler (*Mem. Dept. Agric. India, Bot. Ser.* 1: pl. VIII, figs 1–12, 1907; lectotype designated by Dick 2001: 374).

Description: “Sporangia formed in the hyphae of the host, irregular in shape, terminal and intercalary, averaging 23 µm in diameter, with a single papilla; zoosporos oblates, with a single cillum borne posteriorly, [resting] spores single, free in the cavity of the host-filament which is enlarged to contain them, numerous, 11–15 µm in diameter, spherical, of pale yellow color, with a moderately thick wall, provided with short regular spines, germination not observed” (Butler 1907).

Hosts: *Pythium (?) vexans*, and *Pythium sp.* (*Oomycota*).

Note: Karling (1981) observed a species he tentatively identified as *R. irregularis* in *Pythium debaryanum*, and on the basis of his observations and those of others (Butler 1907, Shen & Siang 1948), he expanded the diagnosis of the species.

*Rozella itersoniliae* D. J. S. Barr & Bandoni, *Mycologia* 71: 1261 (1979).

Synonym: *Pleotrachelus itersoniliae* (D. J. S. Barr & Bandoni) M. W. Dick, *Stramin. Fungi* 453 (2001).

Type: Barr & Bandoni (*Mycologia* 71: 1262, figs 1–4, 1979; – holotype).

Description: “Sporangium endobiotic with no definite wall. Zoosporos globose, 2.0–2.5 µm diameter, posteriorly uniflagellate; whiplash flagellum 11–13 µm long. Resting spores not seen” (Barr & Bandoni 1979).

Host: *Itersonilia perplexans* (*Basidiomycota*).

*Rozella laevis* Karling ex Letcher, sp. nov. MycoBank MB828495

Synonym: *Rozella laevis* Karling, *Mycologia* 34: 201 (1942); nom. inval. (Arts. 39.1, 40.1).

Type: Karling (*Mycologia* 36: 642, figs 1–19, 1944 – holotype).

Description: “Sporangium solitary, partly or completely filling hypertrophied portions of the host hyphae, variable in size and shape, spherical, 20–52 µm, clavate, 10–20 µm × 30–112 µm, broadly and elongately pyriform with 1 to 3 exit papillae, 3–4 µm in diameter, by 2–3 µm in height. Zoosporos hyaline, with a globular spot that is not markedly refractive, obclavate to pyriform, 1.5–1.8 µm × 2.9–3.3 µm; ...flagellum 10–12 µm long. Resting spores spherical, 11–18 µm, oval, elongate or obpyriform with a large central vacuole and coarsely granular cytoplasm; wall smooth and hyaline, 1.5–2 µm thick; germination unknown” (Karling 1942b).

Hosts: *Pythium gracile*, and *Pythium sp.* (*Oomycota*).

Note: The original description (Karling 1942) lacked illustrations, so the species is typified by illustrations from a later work (Karling 1944) by the same author.

*Rozella longicollis* Karling, *Sydowia* 19: 218 (1965).

Type: Karling (*Sydowia* 19: pl. XLVI, figs 21–29, 1965; lectotype designated by Dick 2001: 375).

Description: “Sporangia solitary, filling the host sporangia, spherical, 20–60 µm diameter, pyriform, ovoid, 15–18 × 22–35 µm, with 1–5 straight or curved exit tubes, 7–15 µm long by 3–3.7 µm diameter, which project beyond surface of host cell. Zoosporos broadly pyriform while motile, 1.5–2 × 2.5–3 µm, with a slightly tapering anterior end and a minute dense body in the cytoplasm; flagellum 12–14 µm long; swirling in...
the sporangium before emerging. Resting spores filling only a portion of host cell, dark-brown, ovoid to spherical, 12–17 µm diameter, wall punctate to spiny, rarely smooth; germination unknown” (Karling 1965).

Host: *Pythium* sp. (*Oomycota*).

**Rozella longisporangia** Willoughby & R. Rigg, *Nova Hedwigia* 37: 378 (1983).

Type: Willoughby & Rigg, *Nova Hedwigia* 37: 377, fig. 1, 1983; *lectotype designated here*, MBT 384209).

Description: “Sporangia spherical, single, 15.2–42.2 µm diameter, or fused in pairs, or cymbiform, 50–72 µm long × 10–21 µm wide, or spherical with cylindrical extensions up to 53 µm long × 5.3–7 µm wide, or cylindrical only, up to 170 × 5.3–7 µm. Sporangia with 1–4 dehiscence papillae, 3.8–6.8 µm across. Zoospores liberated following liquefaction of the papillae. Zoospores swarm together in the sporangium before they disperse. Zoospores with hyaline oil drops, with a posterior flagellum 10.6–11.4 µm long, ovoid when in motion, spherical when at rest, 3–4 µm diameter. Resting spores not observed” (Willoughby & Rigg 1983).

Host: *Pythium oligandrum* (*Oomycota*).

**Rozella marina** (Sparrow) Sparrow, *Mycologia* 30: 377 (1938).

Basionym: *Pleolpidium marinum* Sparrow, *Biol. Bull. Mar. Biol. Lab. Woods Hole* 70: 256 (1936).

Type: Sparrow (*Biol. Bull. Mar. Biol. Lab. Woods Hole* 70: figs 32–33, 1936; *lectotype designated here*, MBT 384211).

Description: “Sporangium spherical, completely filling the enlarged host sporangium, 30–45 µm in diameter, at maturity forming from one to three pores, through which the zoospores are discharged; zoospores ellipsoidal, 3 µm long by 2 µm in diameter, posteriorly uniflagellate, without globules; resting spore not observed” (Sparrow 1960).

Host: *Algochytrops polysiphoniae* (*Chytridiomycota*).

Note: In addition to Sparrow’s observations (Sparrow 1936b, 1938), *R. marina* was observed in the same host from Iceland (Johnson 1966).

**Rozella monoblepharis** Cornu, *Ann. Sciences Nat.*, *Bot. sér. 5*, 15: 150 (1872).

Synonyms: *Rozella monoblepharis-polymorpha* Cornu *Ann. Sciences Nat.*, *Bot. sér. 5*, 15: 150 (1872).

*Pleolpidium monoblepharis-polymorpha* (Cornu). A. Fischer, *Rabenh. Krypt.-Fl.* 1 (4): 44 (1892).

Type: Cornu (*Ann. Sci. Nat.*, *Bot. sér. 5*, 15: pl. 4, figs 13–18, 1872; lectotype designated by Dick 2001: 373).

Description: “Sporangia formed in intercalary swollen parts of the hyphae, ovoid … with a single small lateral discharge pore; zoospores not observed; resting spore spherical, brown, the thickened wall densely covered with tenuous spines, in intercalary or lateral swellings of the host hyphae, germination not observed” (Sparrow 1960).

Hosts: *Monoblepharis polymorpha*, and *M. macrandra* (*Monoblepharamycota*).

**Rozella polymorpha** Letcher & Longcore, *J. Euk. Microbiol.* 64: 183 (2018).

Type: Letcher *et al.* (*J. Euk. Microbiol.* 65: 182, fig. 1, 2018 – holotype).

Description: Sporangia are monosporangiate, spherical, typically 15–20 µm diameter, rarely to 50 µm diameter, pyriform, or irregularly-shaped, with (typically) one to three discharge tubes ~ 2 µm diameter × 5–40 µm long, the discharge tube terminating with a constriction and bulb-shaped structure. Zoospores are elongate, 1.1–1.2 µm diameter × 1.6–1.8 µm long, containing a helmet-shaped nucleus, a microbody-lipid globule complex composed of a single mitochondrion, a pair of lipid globules, a microbody, and a backing membrane. Zoospores are immotile in the sporangium prior to release, and are released as a mass of motile spores that rapidly disperse. Resting spores not observed (Letcher *et al.* 2018).

Host: *Pythium catenulatum* (*Oomycota*).

**Rozella parva** Canter, *Bot. J. Linn. Soc.* 62: 275 (1969).

Type: Canter (*Bot. J. Linn. Soc.* 62: 275, type material IM 131673 – holotype).

Description: “Sporangium solitary assuming the shape of the unhypertrophied host sporangium or young resting spore. Sporangium usually spherical 4–9.5 µm diameter, with one hyaline dehiscence papilla … Up to 12 zoospores in a sporangium emerging singly on dehiscence and immediately swimming away. Zoospore 2.5 µm diameter, sometimes pyriform 1.8 × 3.5 µm, broad anterior end when swimming. Within the content are two to five anteriorly placed, minute refractive granules; flagellum posterior 12.5 µm long, with a short whiplash. Resting spore more or less spherical 5–10.6 µm diameter with a thick refractive wall, on the outside of which may be deposited lumps of solid material, or an apparently thin corrugated undulate external wall. Within the resting spore is a large hyaline sphere and many small refractive globules” (Canter 1969).

Host: *Zygorhizidium affluens* (*Chytridiomycota*).

**Rozella polyphagi** (Sparrow) Sparrow, *Mycologia* 30: 377 (1938).

Basionym: *Pleolpidium polyphagi* Sparrow, *Trans. Brit. Mycol. Soc.* 18: 215 (1933).

Type: Sparrow (*J. Linn. Soc.*, *Bot.* 50: pl. 14, figs 19–20, 1936; neotype designated by Dick 2001: 374, as “lectotype”, drawn from the same material used in Sparrow 1933).
Description: "Sporangium colorless, spherical, completely filling the often markedly swollen prosorogium of the host, 20–48 µm in diameter, possessing at maturity from two to six prominent papillae 4–8 µm in diameter, through which in innumerable minute posteriorly uniflagellate narrowly ovoid zoospores 2–3 µm long by 1.5–2 µm in diameter, with a single globule, are discharged; resting spore not observed (Sparrow 1960).

Host: Polyphagus laevis (Chytridiomycota).

Note: Ultrastructure of the thallus of R. polyphagi has been studied (Powell 1984).

Rozella pseudomorpha (Scherff.) Sparrow, *Aquatic Phycom.*: 124 (1943).

Synonym: Olpidium (?) pseudomorphum Scherff., *Arch. Protistenk.* 54: 510 (1926).

Type: Scherffel (*Arch. Protistenk.* 54: taf. 28, figs. 1–5, 1926; *lectotype designated here*, MBT 384214).

Description: "Sporangium filling the vegetative cell of the host, and hence assuming its shape and size, forming a fairly stout tapering discharge tube; zoospores narrowly ellipsoidal, ovoid, or plump and rod-like, somewhat arched, with from three to five refractive granules, flagellum fairly long, trailing, attached at the concave side of the body, zoospores emerging individually from the discharge tube and remaining for a time near the orifice undergoing amoeboid change in shape, movement hopping; resting spore unknown" (Sparrow 1960).

Host: Lagenidium rabenhorstii (Oomycota).

Note: Sparrow (1960) stated "that the sporangium fills the vegetative cells of the host". We accept *R. pseudomorpha* here because of the posteriorly uniflagellate zoospore.*

Rozella rhizophlyctis Karling, *Amer. J. Bot.* 29: 32 (1942); as "rhizophlyctis".

Type: Karling (*Amer. J. Bot.* 29: 30, figs 36–47, 1942; *lectotype designated by Dick 2001: 375).

Description: "Sporangia solitary, filling host cell and conforming with the latter’s size and shape, spherical, 20–110 µm, oval, and irregular with 1 to 4 exit papillae which usually project out of the short necks of the host; ... zoospores hyaline, broadly pyriform, 2.5–3 µm × 1.5–2 µm, tapering slightly at the anterior end, with a minute globule near the posterior end; posteriorly uniflagellate, ... flagellum 16–18 µm long; swirling in the sporangium before emerging; darting about rapidly in swimming, occasionally becoming amoeboid. Resting spores slightly yellow, oval and spherical, 14–18 µm in diameter, with a large central vacuole and coarsely granular cytoplasm; wall spiny, 1.8 µm thick, spines 1.5–2 µm long; apparently transformed directly into a zoosporangium in germination and forming zoospores" (Karling 1942a).

Hosts: Rhizophlyctis petersenii, and R. rosea (Chytridiomycota).

Rozella rhizophydii Karling, *Mycologia* 36: 645 (1944).

Type: Karling (*Mycologia* 36: 645, figs 20–28, 1944; *lectotype designated by Dick 2001: 375).

Description: "Sporangia solitary, filling host cell and conforming with the latter’s size and shape, spherical, 15–30 µm, oval, 10–12 µm × 13–20 µm or pyriform, 12–15 µm × 16–25 µm with 1–3 low exit papillae; ... zoospores hyaline, oval or slightly pyriform, 2–2.5 µm × 3–4 µm; with a small globule near the posterior end; flagellum 12–14 µm long. Resting spores unknown" (Karling 1944).

Host: Rhizophydium globosum (Chytridiomycota).
Rozella septigena Cornu, Ann. Sci. Nat., Bot., sér. 5, 15: 163 (1872).

**Synonym**: Skiriellia septigena (Cornu) A. Batko, Acta Mycol. 13:322 (1977); nom. illegit. (Arts. 52.1, 52.2).

**Type**: Cornu (Ann. Sci. Nat., Bot. sér. 5: 15; pl. 6, figs. 1-17, 1872).

**Description**: “Sporangia possibly formed by successive fractionation of one thallus, in transversely or obliquely walled-off segments of the sometimes slightly swollen host hyphae which they completely fill, with from one to several discharge papillae; zoospores minute, numerous, arched, posteriorly uniflagellate, without globules; resting spore spherical, with a slightly thickened wall covered with short tenuous spines, brownish, with dense contents, formed in spherically swollen short lateral branches of the hyphae, which are continuous with the main axis or separated from it by a cross wall, germination not observed” (Sparrow 1960).

**KEY TO THE SPECIES OF ROZELLA**

1. Thallus polysporangiate ................................................................. 2
   Thallus monosporangiate .............................................................. 4

2 (1) Host: Oomycota ......................................................................... 3
   Host: Blastocladiomycota: Allomyces ........................................... allomycetis

3 (2) Host: Saprolegnia ....................................................................... septigena
   Host: Achlya and Dictyuchus ......................................................... achlyae

4 (1) Host: Blastocladiomycota: Blastocladiad ..................................... blastocladiad
   Host: Monoblepharidomycota: Monoblepharis ............................... monoblepharisid
   Host: Basidiomycota: Itersonilia ..................................................... itersoniliae
   Host: Coleochaetophyta: Coleochaete ............................................ coleochaetes
   Host: Oomycota ............................................................................. 5
   Host: Chytridiomycota ................................................................. 11

5 (4) Host: Araiospora ........................................................................ rhipidii
   Host: Apodachyla ......................................................................... apodyae
   Host: Pythium ............................................................................. 6
   Host: Lagendidium ........................................................................ pseudomorpha

6 (5) Resting spore present ............................................................... 7
   Resting spore absent .................................................................... 10

7 (6) Resting spore smooth ................................................................ 8
   Resting spore spiny .................................................................... 9

8 (7) Host: P. gracile; resting spore hyaline ........................................ laevis
   Host: P. intermedium, P. monospernum; resting spore pale yellow ...... cuculus

9 (7) Host: P. vexans; resting spore pale yellow .................................. irregularis
   Host: Pythium sp., resting spore dark brown .................................. longicollis

10 (6) Host: P. oligandrum ............................................................... longisporangia
   Host: P. catenulatum ................................................................ multimorpha

**Hosts**: Achlya, Saprolegnia (Oomycota).

**Note**: This species was designated as the type of the genus by Clements & Shear 1931: 234. “Cornu’s name was applied, in error, by Fischer (1882: 365) to a similar-appearing parasite in Saprolegnia which forms biflagellate zoospores” (Sparrow 1960).

**Doubtful and excluded species**

Rozella barrettii Karling, Mycologia 34: 202 (1942). “Based on an incompletely known form described by Barrett (1934: 1138). Since the flagellation of the zoospores is not known, the fungus cannot be placed generically” (Sparrow 1960: 180).

Rozella maxima Karling, Amer. J. Bot. 29: 24 (1942); as “maximum”.

Apparently a typographical error for R. marina (q.v.).
11 (4) Host: Diplophlyctis ...................... diplophlyctidis
Host: Rhizophyctis ......................... rhizophyctidis
Host: Chytriomycetes ...................... chytriomycetis
Host: Polyphagus ......................... polyphagi
Host: Endochytrium ....................... endochytrii
Host: Cladochrytium, Nowakowskiella ........................................ cladochryti
Host: Rhizophydiwm ....................... rhizophydi
Host: Zygochrytium ......................... parva
Host: Rhizoclosmatium ...................... rhizoclosmati
Host: Chytidium ......................... canerae
Host: Algochrytrops ................................ marina

ACKNOWLEDGEMENTS

This study was supported by the National Science Foundation through MRI DEB-0500766 and DEB-1455611. We very much appreciate Shaun Pennycook (Landcare Research, New Zealand) for his assistance with nomenclatural issues.

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