Check-list of microscopic protosteloid amoebae from the Southwest of Europe

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Abstract

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A biodiversity survey for protosteloid amoebae was carried out in Spain, Portugal and France between 2005 and 2010. Samples were collected from three different microhabitats – aerial litter, ground litter, and bark of living plants – in a total of 97 localities. As result 26 to 28 species out of the 33 species of microscopic protosteloid amoebae described to date were recorded. An annotated list that comprises all available data about these organisms from this part of the world, a key to the species, comments on the morphology of the sporocarps and the trophic stages is presented. Photomicrographs of the fruiting bodies of most species, and distribution maps are also included.

Keywords: Protostelids, morphology, taxonomy, distribution, Iberian Peninsula, protists, Amoebozoa.

INTRODUCTION

Protosteloid amoebae, also known as protostelids, are a group of heterotrophic unicellular organisms occurring on dead aerial plant parts, bark, leaf litter, herbivore dung, and soil. They have been observed from collections made throughout the world (Olive, 1975; Moore & Spiegel, 1995, 2000c; Moore & al., 2000; Spiegel & Stephenson, 2000; Shadwick & Stephenson, 2004; Spiegel & al., 2004; Tesmer & al., 2005; Powers & Stephenson, 2006; Kosheleva & al., 2009; Ndiritu & al., 2009). For a recent comparison of published biodiversity studies on a global scale we recommend consulting Table 2 in Ndiritu & al. (2009).

Their trophic stages vary from uninucleate amoeboid and/or amoeboflagellate cells to multinucleate reticulate plasmodia. Their major defining characteristic is that they form fruiting bodies or sporocarps. Sporocarps develop from a single amoeboid cell and, at maturity, are comprised of a single acellular stalk and one to a few spores (Olive, 1975; Spiegel, 1986, 1990; Spiegel & al., 2004). They probably have an important role in the regulation of the populations of bacteria present in soils and other microhabitats in terrestrial ecosystems (Feest, 1987; Spiegel & al. 2004), where they take part as predators feeding also upon other decomposers such as veasts, and filamentous fungi (Olive, 1975; Whitney & Bennett, 1984). These organisms were traditionally classified as occupying a primitive position within the group of slime molds termed Eumycetozoa, that also includes the myxomycetes and the dictyostelids (Olive, 1975; Spiegel, 1986; Spiegel Lee & Rusk, 1995; Baldauf & Doolittle, 1997), but recent molecular data suggest that protosteloid amoebae are

Resumen

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Se ha realizado un estudio de la biodiversidad de las amebas protosteloides en España, Portugal y Francia entre 2005 y 2010. Las muestras se recolectaron en tres microhábitats diferentes –hojarasca aérea, hojarasca del suelo y corteza de plantas vivas— en un total de 97 localidades. Como resultado se encontraron entre 26 y 28 especies de las 33 especies de amebas protosteloides microscópicas descritas. Se presenta una lista comentada que contiene todos los datos disponibles sobre estos organismos en esta parte del mundo, una clave de las especies y comentarios sobre la morfología de los esporocarpos y de los estados tróficos. También se incluyen fotomicrografías de los cuerpos fructíferos de la mayoría de las especies y mapas de distribución.

Palabras clave: Protostélidos, morfología, taxonomía, distribución, Península Ibérica, protistas, Amoebozoa.

polyphyletic and they belong to different groups of Amoebozoa (Shadwick & al., 2009b; Fiore-Donno & al., 2010; Lahr & al., 2011; Adl & al., 2012), not necessarily directly related to other eumycetozoans.

Several surveys have been carried out in temperate areas (Best & Spiegel, 1984; Moore & Spiegel, 1995, 2000a, 2000b; Shadwick & Stephenson, 2004; Tesmer & al., 2005; Aguilar & al., 2007; Brown & Spiegel, 2008; Shadwick & al., 2009a), tropical regions (Stephenson & al., 1999; Moore & Spiegel, 2000c; Moore & Stephenson, 2003; Powers & Stephenson, 2006; Ndiritu & al., 2009), boreal regions (Spiegel & Stephenson, 2000; Moore & al., 2000; Kosheleva & al., 2009), and aquatic environments (Lindley & al., 2007; Tessmer & Schnittler, 2009). However, it is remarkable that Europe, one of the territories most extensively studied for the great majority of organisms, has barely been surveyed for protosteloid amoebae. Only one investigation was made in beech forests in northeastern Germany (Tesmer & al., 2005), one in oak forests of Ukraine (Glustchenko & al., 2002), and one in taiga forest and steppe of Russia (Kosheleva & al., 2009).

The Iberian Peninsula has previously proved to be an excellent location for other groups of slime moulds, such as Dictyostelids (Romeralo & Lado, 2006) and Myxomycetes (Lado & Pando, 1997), and its special features like an accentuated and varied relief, and its varied vegetation and climate produce a high diversity of ecosystems to be colonized by slime molds. It is also characterized by the longlasting influence of humans, constituting a mosaic of successional stages. The study of protostelids in such a wide variety of habitats can help to increase available information about their diversity patterns in areas with temperate climates.

Table 1. Classification of protosteloid amoebae based on Spiegel (1990), Shadwick & al. (2009), Lahr & al. (2011) and Adl & al. (2012).

Amoebozoan group	Protosteloid genera included				
Protosteliida Olive & Stoianovitch 1966, emend. Shadwick & Spiegel in Adl & al. 2012	Planoprotostelium, Protostelium				
Cavosteliida Shadwick & Spiegel in Adl & al. 2012	Cavostelium, Schizoplasmodiopsis, Tychosporium				
Protosporangiida Shadwick & Spiegel in Adl & al. 2012	Clastostelium, Protosporangium				
Fractovitelliida Lahr & al. 2011	Soliformovum				
Schizoplasmodiida L. Shadwick & Spiegel in Adl & al. 2012.	Ceratiomyxella, Nematostelium, Schizoplasmodium				
Vannellida Smirnov & al. 2005	Protosteliopsis fimicola				
Pellitida Smirnov & al. 2011 or incertae sedis Himatismenida	Endostelium				
Incertae sedis Centramoebida	one undescribed protosteloid LHI05, and perhaps also "Protostelium" arachisporum and "Protostelium" pyriforme.				
Incertae sedis Amoebozoa	Echinosteliopsis, Microglomus				

We present here an annotated list of the microscopic protostelid species (i.e excluding *Ceratiomyxa*) recorded to date in the southwest of Europe that comprises all available data from this part of the world. Before the beginning of this survey there was no previous information about this group in the study area. This check-list is the result of several sampling efforts carried out between 2005 and 2010 by the authors. Some records have been previously published in Aguilar & al. (2007) and Aguilar & al. (2011); the remainder have not been previously published.

MATERIAL AND METHODS

Samples were collected between 2005 and 2010 in a total of 97 localities (Fig. 1, Appendix 1) in Spain (91), Portugal (4) and France (2). All localities were geo-referenced through the use of a portable GPS unit (model Garmin 12, datum WGS 84). Collections of samples were segregated according to microhabitat type – ground litter (layer of twigs, leaves, and other plant debris extending over the soil surface), aerial litter (assemblage of dead but still attached parts of standing plants) or bark. Samples were placed in separate paper bags, air dried and stored with the codes shown in Appendix 1 in the laboratory of the Real Jardín Botánico.



Fig. 1. Sampled localities (see Appendix 1 for details).

More than 800 primary isolation culture plates were prepared using a modification of the technique described by Olive (1975) and Spiegel & al. (2004), see also Moore & Spiegel (1995), Spiegel & al. (2007) and Aguilar & al. (2011). The material was cut into small (ca. 1.5-2 cm) pieces with sterile scissors. Thirty-two pieces from each sample were plated out in 8 lines of four pieces forming a circle on a 9 cm Petri dish with a weakly nutrient medium (wMY: 0.002g malt extract, 0.002g yeast extract, 0.75g K₂HPO₄, 15g agar/L of distilled water). The material was moistened with a pipette with sterile water just after they were plated out. The plates were incubated at 21 °C and were surveyed for protostelids during the second week of culture.

Species were identified on the basis of fruiting body morphology under the light microscope using Spiegel (1990), Spiegel & al. (2007) and original descriptions. Nomenclature used herein follows Olive (1975) and Lado (2011). Photomicrographs were taken with a Nikon Eclipse 80i compound microscope using bright field optics and a Nikon Digital Sight DS-5M digital camera head.

TAXONOMIC TREATMENT

A total of 26-28 species of protosteloid amoebae were recorded. Species and comments are listed below. The number of species is given as a range because it is likely the presence of various species indistinguishable from their fruiting body morphology (see comments below). Measures and descriptions of trophic stages are based on existing literature, so we recommend consulting the original papers, Spiegel (1990), and Spiegel & al. (2007) for further information and illustrations. Organisms denoted with an asterisk (*) were previously published as new records for Europe in Aguilar & al. (2007) or Aguilar & Lado (2012), while species with two asterisks (**) are previously unpublished new records for the European continent. Distribution maps (Fig. 2) and photomicrographs of the fruiting bodies of most species (Fig. 3) are also provided. See also Appendix 1 for locality details and Table 1 species classification based on Spiegel (1990), Shadwick & al. (2009), Lahr & al. (2011), and Adl & al. (2012).

KEY TO THE SPECIES

1.	Stalks usually shorter than two spore diameters
	More than one spore
2.	One spore
3.	The upper portion of the stalk forms an articulation that bends in air
_	currents. Two to four spores \dots 10. Protosporangium articulatum
3.	The upper portion of the stalk does not form an articulation that
	bends in air currents
4.	Stalk long, flexuous and easily fragmented. Usually four spores in a
	nearly spherical tetrad
4.	Stalks very long, thin and flexuous. Two (rarely one) spores in a near-
Е	ly spherical dyad
Э. Е	Prespore cells not "fried-egg" shaped
	Spores spherical, often American football shaped when dried, broad
Ο.	long straight to gently curved stalk, not tapering but with hastate
	apophysis at the tip
6	Spores spherical, stalk bipartite with a reflexed, broadly tapered basal
0.	section and a uniformly thin apical section
	24. Soliformovum expulsum
7	Yellowish or brownish sporocarps, with beaded stalks and obpyri-
	form spores irregular in shape
7	Sporocarps without beaded stalks
8.	Spores strongly warted or with a reticulated surface
8.	Spores with a smooth surface
9.	Broad stalk with a distinct knob like apophysis. Spores irregular in
	shape strongly warted 5. Endostelium amerosporum
9.	Reticulated spores 21. Schizoplasmodiopsis reticulata
	Peanut shaped or obpyriform spores
10.	Spores round or elliptical in outline
11.	Obpyriform spores on an unbeaded stalk
	17. Protostelium pyriforme
11.	Peanut-shaped to ellipsoid spores
	13. Protostelium arachisporum
12.	Stalks with a distinct knob-like apophysis and a ring-like hilum on the
12	spore where it articulates with the stalk
	Stalks without a distinct knob-like apophysis
	Spores ovate to elliptical in outline 9. Nematostelium ovatum
15.	Spores round in outlin
14	Very small (15-25 μm), ballistosporous sporocarps. It has a round
	apophysis that bursts together with the spore; leaving fields of stalks
	resembling stubble-like hairs 16. Protostelium okumukumu
14.	Bigger sporocarps (usually >25 μm), without a round apophysis . 16
15.	
15.	Nondeciduous spores
16.	Small sporocarps (usually 25-35 µm) that move in air currents, more
	frequently observed after the sunset
16	15. Protostelium nocturnum
10.	Sporocarps with stalks that bend readily in air currents, very variable
10.	Sporocarps with stalks that bend readily in air currents, very variable in size
	Sporocarps with stalks that bend readily in air currents, very variable in size
	Sporocarps with stalks that bend readily in air currents, very variable in size
17.	Sporocarps with stalks that bend readily in air currents, very variable in size
17.	Sporocarps with stalks that bend readily in air currents, very variable in size
17. 17.	Sporocarps with stalks that bend readily in air currents, very variable in size
17. 17. 18.	Sporocarps with stalks that bend readily in air currents, very variable in size
17. 17. 18. 18.	Sporocarps with stalks that bend readily in air currents, very variable in size
17. 17. 18. 18.	Sporocarps with stalks that bend readily in air currents, very variable in size
17. 17. 18. 18. 19.	Sporocarps with stalks that bend readily in air currents, very variable in size
17. 17. 18. 18. 19.	Sporocarps with stalks that bend readily in air currents, very variable in size
17. 17. 18. 18. 19.	Sporocarps with stalks that bend readily in air currents, very variable in size
17. 17. 18. 18. 19.	Sporocarps with stalks that bend readily in air currents, very variable in size
17. 17. 18. 18. 19.	Sporocarps with stalks that bend readily in air currents, very variable in size
17. 17. 18. 18. 19.	Sporocarps with stalks that bend readily in air currents, very variable in size
17. 17. 18. 18. 19.	Sporocarps with stalks that bend readily in air currents, very variable in size
17. 17. 18. 19. 19.	Sporocarps with stalks that bend readily in air currents, very variable in size
17. 17. 18. 19. 19.	Sporocarps with stalks that bend readily in air currents, very variable in size
17. 17. 18. 18. 19. 20. 20.	Sporocarps with stalks that bend readily in air currents, very variable in size
17. 17. 18. 18. 19. 20. 20.	Sporocarps with stalks that bend readily in air currents, very variable in size

22. Without a cup-shaped apophysis2!
23. Undeciduous, slightly ornamentated spore
1. Cavostelium apophysatun
23. Ballistosporic, spore unornamented, with hilum where it articulate
with stalk 23. Schizoplasmodium cavostelioide
24. Stalk tapered to form an acute point
18. Schizoplasmodiopsis amoeboide
24. Stalk not tapered to form an acute point
25. Spherical spores with subtle lumps in their walls., Stalks can be eithe
long or short, and often very coarse in appearance
22. Schizoplasmodiopsis vulgari
25. Spores without lumps
20. Schizoplasmodiopsis pseudoendospora

1. *Cavostelium apophysatum L.S. Olive, Mycologia 56(6): 886. 1965 ("1964"). Figs. 2a, 3a

Sporocarps. Sporocarps 8-23 µm tall. Very short stalks, 3.2-10.5 µm long, with a distinct, cup-like apophysis measuring from one third to more than one half of the total length of the stalk. The apophysis is usually wider than the base of the stalk, but sometimes it is narrower and the stalk seems to be equally thick for its entire length. Spores rough, colorless, nearly spherical, 4.8-12.6 µm diam., with spines and warts on their surface. Prespore cells are circular in outline (Spiegel & al., 2007).

Trophic stages. It grows well on bacterial cultures including Serratia liquefaciens strain Florida 20 on wMY agar. The amoeboflagellates typically have one single nucleus and one to several contractile vacuoles, and their sub-pseudopodia are filose. When amoeboflagellates are in water, they can develop usually one but quite often two (more rarely three or four) flagella, cells mostly 5-13 \times 14-32.5 μ m (Olive, 1964). The amoeboflagellate state eventually develops into an obligate amoeba that is unable to produce flagella (Spiegel & Feldman, 1985). Obligate amoebae are uninucleate and flat, elliptical to fan-shaped, and typically angular in outline. They may form acutely pointed, narrow pseudopodia. When they move, they can be divided into branches (Spiegel & Feldman, 1985). The cysts are spherical to oval or somewhat irregular in shape, 4.3-23 µm in diam. (Olive, 1964). Encystment is infrequent in obligate amoebae. See Spiegel & Feldman (1985) for illustrations.

Though it is usually a common species in the tropics and relatively uncommon in temperate climates (Spiegel & al., 2007; Ndiritu & al., 2009), it was quite abundant in our study area. In Europe, it has been also cited from Russia (Kosheleva & al., 2009).

Specimens examined

Loc. 1: ground litter of Compositae, AS05-12. Loc. 3: aerial litter of Lamiaceae, AS05-39. Loc. 6: bark of Fagus sylvatica, AS05-66; aerial litter of Erica sp., AS05-68. Loc. 9: ground litter of Cytisus sp., AS05-84. Loc. 11: ground litter of Tilia sp., AS05-105. Loc. 13: ground litter of Lavandula sp., M06-32; aerial litter of Thymus sp., M06-33; ground litter of Thymus sp., M06-34; aerial litter of Quercus ilex, M06-35; aerial litter of Genista scorpius, M06-37; ground litter of G. scorpius, M06-38. Loc. 14: ground litter of Retama sphaerocarpa, M06-44. Loc. 15: ground litter of Leguminosae, GU06-04; ground litter of Lavandula sp., GU06-06. Loc. 16: ground litter of Quercus coccifera, GU06-08; aerial litter of Leguminosae, GU06-10. Loc. 17: aerial litter of Gramineae, GU06-11; ground litter of Gramineae, GU06-12; aerial litter of Rosmarinus officinalis, GU06-13; ground litter of R. officinalis, GU06-14; aerial litter of Q. coccifera, GU06-15.

Loc. 18: ground litter of Gramineae, CU06-02. Loc. 19: aerial litter of Gramineae, CU06-05; ground litter of Gramineae, CU06-06; aerial litter of Thymus sp., CU06-07; ground litter of Thymus sp., CU06-08. Loc. 20: aerial litter of Q. ilex, M07-05. Loc. 21: aerial litter of Cistus salvifolius, M07-13; ground litter of C. salvifolius, M07-14; ground litter of Gramineae, M07-16; aerial litter of Lavandula sp., M07-17; ground litter of Lavandula sp., M07-18; bark of Q. ilex, M07-19. Loc. 22: aerial litter of Q. ilex, AV07-03; aerial litter of Juniperus oxycedrus, AV07-07; ground litter of J. oxycedrus, AV07-08; bark of Q. ilex, AV07-09; bark of J. oxycedrus, AV07-10. Loc. 23: aerial litter of Q. ilex, TO07-01; ground litter of Q. ilex, TO07-02; ground litter of R. sphaerocarpa, TO07-04; aerial litter of J. oxycedrus, TO07-05; ground litter of J. oxycedrus, TO07-06; aerial litter of Lavandula sp., TO07-07; ground litter of Lavandula sp., TO07-08; bark of Q. ilex, TO07-10. Loc. 24: ground litter of Cistus ladanifer, AV07-12, aerial litter of Quercus pyrenaica, AV07-13, ground litter of *Q. pyrenaica*, AV07-14, aerial litter of *Q. ilex*, AV07-17. **Loc.** 25: aerial litter of Q. ilex, TO07-11; aerial litter of thistle, TO07-13; aerial litter of C. ladanifer, TO07-15; ground litter of Lavandula sp., TO07-18; bark of O. ilex, TO07-20. Loc. 26: ground litter of Leguminosae, GU07-06; bark of J. oxycedrus, GU07-09. Loc. 27: aerial litter of Juniperus thurifera, GU07-13; ground litter of Juniperus thurifera, GU07-14; aerial litter of Lavandula sp., GU07-15; bark of Juniperus sp., GU07-16; ground litter of Leguminosae, GU07-18; bark of Ulmus sp., GU07-20. Loc. 28: ground litter of Lamiaceae, TE07-20; bark of O. faginea, TE07-27. Loc. 29: ground litter of Erinacea anthyllis, TE07-29. Loc. 31: bark of Olea europaea, TE07-52. Loc. 32: ground litter of R. officinalis, Z07-02; bark of J. phoenicea, Z07-09. Loc. 33: ground litter of Gramineae, Z07-14; bark of R. officinalis, Z07-15; bark of Pinus halepensis, Z07-16; ground litter of Pistacia lentiscus, Z07-20. Loc. 34: ground litter of R. officinalis, Z07-22; bark of Juniperus sp., Z07-23; ground litter of P. halepensis, Z07-28. Loc. 35: aerial litter of Lygeum spartum, Z07-31; aerial litter of Arthrocnemum sp., Z07-33; ground litter of Arthrocnemum sp., Z07-34; aerial litter of Suaeda sp., Z07-36; ground litter of Salsola sp., Z07-38. Loc. 36: aerial litter of L. spartum, HU01-01; ground litter of L. spartum, HU01-02; ground litter of Compositae, HU01-06; bark of R. officinalis, HU01-09; bark of J. phoenicea, HU01-10. Loc. 37: aerial litter of Ulex sp., HU01-14; bark of Quercus faginea, HU01-19. Loc. 45: aerial litter of Leguminosae, NA07-23; aerial litter of Atriplex halimus, NA07-33; ground litter of Atriplex halimus, NA07-34. Loc. 47: aerial litter of Lamiaceae, SO07-09; ground litter of Lamiaceae, SO07-10. Loc. 49: ground litter of R. officinalis, CU07-02; aerial litter of Cistus albifolius, CU07-05; ground litter of Cistus albifolius, CU07-06; aerial litter of Gramineae, CU07-07; bark of O. ilex, CU07-09; bark of J. oxycedrus, CU07-10. Loc. 50: ground litter of Compositae, CU07-14; aerial litter of Q. ilex, CU07-15; ground litter of Q. ilex, CU07-17litter of Leguminosae, M06-26. Loc. 62: aerial litter of Epilobium hirsutum and Lithrum salicaria, O06-01; ground litter of Epilobium hirsutum and Lithrum salicaria, O06-02. Loc. 66: ground litter of Leguminosae, LE06-04. Loc. 68: aerial litter, AL07-01. Loc. 73: ground litter of Erica sp., GE08-04; aerial litter of Acer monspessulanum, GE08-07; bark of Erica sp., GE08-09. Loc. 74: aerial litter of Rosaceae, GE08-17; bark of Quercus sp., GE08-19. Loc. 78: aerial litter of Gramineae, CA09-31. Loc. 80: aerial litter of Cistus sp., BA09-21. Loc. 81: ground litter of Cistus sp., BA09-22. Loc. 87: aerial litter of Cistus sp., H09-23; aerial litter of Gramineae, H09-25. Loc. 92: aerial litter of Cistus sp., CO09-07.

2. *Clastostelium recurvatum L.S. Olive & Stoian., Trans. Brit. Mycol. Soc. 69(1): 83. 1977. Figs. 2a, 3b

Sporocarps. Sporocarps 20-42 µm tall, with two spores at the tip of a bipartite, recurved stalk. Stalk with a short apiculate base and a longer inflated upper portion that bursts to disperse the spores. The spores are smooth, hemispherical to subglobose, 7.2-12 µm in diam. (Olive & Stoianovitch, 1977a). Prespore cells circular in outline (Spiegel & al., 2007).

Trophic stages. It grows well on either hay infusion or lactose-yeast extract agar at pH 6.5-7 in the presence of Aerobacter aerogenes or Klebsiella pneumoniae (Shadwick & al., 2009b). At germination, each spore liberates one or two flagellate cells or a single amoeboid cell, that can be uninucleate or plurinucleate (Olive & Stoianovitch, 1977a). Obligate amoebae are uni or multinucleate, broad and flat, with broad

pseudopodia with acutely pointed subpseudopodia (Spiegel & Feldman, 1988). The cysts are round to ovate or irregular in outline, uninucleate to plurinucleate, $7.2-47 \times 7.2-61$ µm (Olive & Stoinanovitch, 1977a).

It is a relatively uncommon species that appears to be more frequent in the tropics (Spiegel & al., 2007), and we found it only once in our samples.

Specimens examined

Loc. 74: ground litter of fern, GE08-16.

3. Echinosteliopsis oligospora Reinhardt & Olive, Mycologia 58(6): 967. 1967 ("1966"). Figs. 2b, 3c, d

Sporocarps. Sporocarps 38-88 µm tall. Short stalk, 14-45.5 µm long, broad, straight to slightly curved, that tappers from the base to the tip. Spores usually 4-6, surrounded by a transparent, hygroscopic sheath that, in conditions of high humidity, appears as a spherical structure, 17-48 µm in diam., and in dryer conditions deflates, and the sporangium becomes clover-shaped. Prespore cells are circular in outline (Spiegel & al., 2007).

Trophic stages. It can be cultivated on hay infusion agar along with a food organism, like Flavobacterium sp., Escherichia coli, Aerobacter aerogenes, Serratia liquefaciens strain Florida, Dyadobacter sp. strain Malaya, and a mixture of Phoma conidiigena and Flavobacterium. The spore liberates a single amoeba which is quite broad in movement 28.6-62.1 × 34.5-89.7 µm, and has a distinct hyaloplasmic anterior margin. Posteriorly, fine filose projections are produced. The amoebae are usually uninucleate, but can have up to 4 nuclei with numerous peripheral small nucleoli. No flagellated cells have been observed. The sheath, the spore walls, and the cysts walls give a positive test for cellulose in chloriodide of zinc. The cysts are uninucleate to multinucleate and irregular in outline. See Reinhardt & Olive (1966), and also Lindley & al. (2006) for transmission electron micrographs.

It is common worldwide and sometimes locally abundant (Spiegel & al., 2007). It was also very abundant in some of our cultures. In Europe, this species has been reported previously from Germany (Tesmer & al., 2005) and Russia (Kosheleva & al., 2009).

Specimens examined

Loc. 1: ground litter of Compositae, AS05-12. Loc. 2: aerial litter of *Cytisus* sp., AS05-20. Loc. 3: aerial litter of *Cytisus* sp., AS05-31; aerial litter of *Quercus ilex*, AS05-37. Loc. 11: ground litter of *Rubus* sp., AS05-97; ground litter of *Campanula* sp., AS05-101; ground litter of Compositae, AS05-103; aerial litter of *Tilia* sp., AS05-104. Loc. 17: aerial litter of *R. officinalis*, GU06-13. Loc. 23: aerial litter of *J. oxycedrus* TO07-05. Loc. 43: ground litter of Gramineae, NA07-15. Loc. 62: aerial litter of *Epilobium hirsutum* and *Lithrum salicaria*, O06-01. Loc. 65: aerial litter of *Chamaespartium tridentatum*, LU06-03. Loc. 74: aerial litter of Rosaceae, GE08-17. Loc. 92: aerial litter of Compositae, CO09-05.

4. Echinostelium bisporum (L.S. Olive & Stoian.) K.D. Whitney & L.S. Olive, in Whitney, Bennett & Olive, Mycologia 74(4): 680. 1982. ≡ *Cavostelium bisporum* L.S. Olive & Stoian., Mycologia 58(3): 440. 1966. Figs. 2a, 3 e, f

Sporocarps. Sporocarps very small, 19-26 μ m long, two-spored, with a seath that can be inflated with water in high hu-

midity conditions or stuck to the spores in drier stages. Stalk short, 7-13.5 μ m long, straight to gently curved, and with a pronounced taper from the base to the tip. The upper part of the spore is flattened. Spores 7-10 μ m diam. One spore is directly attached to the stalk and the other is at the top. Prespore cells circular in outline (Spiegel & al., 2007).

Trophic stages. They produce amoebae with lobose pseudopodia, flagellated cells, $4\text{-}6.5 \times 9\text{-}19.5 \,\mu\text{m}$, and a plasmodial stage, $32\text{-}300 \times 54\text{-}500 \,\mu\text{m}$. The flagellar apparatus is identical to that of myxomycetes (Spiegel, 1981), having one or two flagella. The cysts are globose or irregular in shape [4.2-22.5 × 4.2-56 μm] (Olive & Stoianovitch, 1966a). See Spiegel and Feldman (1991) for illustrations.

Though it is common worldwide showing patches of high local abundance (Spiegel & al., 2007), it was not very common in our study. In Europe, it has been previously reported from Germany (Tesmer & al., 2005). This species was first described as a protostelid by Olive & Stoianovitch (1966a) but it was later included in the myxomycetes (Spiegel & Feldman, 1989; Whitney & al., 1982). However, as protosteloid amoebae are recognised solely on the basis of sporocarp morphology and not on any suggestion of relatedness (Shadwick & al., 2009b), *E. bisporum* can be considered as a protosteloid member of the myxomycetes.

Specimens examined

Loc. 2: aerial litter of *Cytisus* sp., AS05-20. Loc. 10: aerial litter of Poaceae, AS05-87. Loc. 11: aerial litter of *Rubus* sp., AS05-96. Loc. 12: ground litter of *Rubus* sp., AS05-110. Loc. 16: aerial litter of Leguminosae, GU06-09. Loc. 22: aerial litter of *Q. ilex*, AV07-03. Loc. 23: bark of *J. oxycedrus*, TO07-09. Loc. 26: ground litter of Leguminosae, GU07-06. Loc. 32: bark of *J. phoenicea*, Z07-09. Loc. 33: ground litter of Gramineae, Z07-14. Loc. 45: ground litter of Leguminosae, NA07-24. Loc. 51: bark of *Pinus nigra*, CU07-29. Loc. 52: ground litter of Leguminosae, CU07-38. Loc. 62: ground litter of *Epilobium hirsutum* and *Lithrum salicaria*, O06-02. Loc. 74: aerial litter of *Fagus sylvatica*, GE08-11; aerial litter of *Castanea sativa*, GE08-13. Loc. 90: aerial litter of *Quercus ilex*, SE09-01.

5. **Endostelium amerosporum L.S. Olive, in Olive, Bennett & Deasey, Mycologia 76(5): 886. 1984. Fig. 2c

Sporocarps. Sporocarps 95-135 µm tall. Stalk 60-87.6 µm, broad, slightly tappered and with a distinct knob-like apophysis at the tip. Spores uninucleate, irregular, from elliptical to spherical in shape, 33.6-51.5 µm diam. (Olive & al., 1984). Spores appear to be strongly warted, maybe due to the presence of bacteria attached to the external surface of the spore wall. Prespore cells are circular in outline (Spiegel & al., 2007).

Trophic stages. It grows on lactose-yeast extract and on oak bark pH 6 agar media with *Flavobacterium* sp. added. The amoeba typically contains a nucleus and a contractile vacuole, and it is uninucleate and surrounded by a sheath that contains small particles, and frequently bacteria. The cysts, 24-38.4 µm, are typically globose, usually surrounded by a scabrous sheath (see Olive & al., 1984).

It is a rare species and has been recorded only a few times (Spiegel & al., 2007), and we found it only in one of our cultures.

Specimens examined

Loc. 28: bark of Q. faginea, TE07-27.

6. *Endostelium zonatum (L.S. Olive & Stoian.) W.E. Benn. & L.S. Olive, in Olive, Bennett & Deasey, Mycologia 76(5): 891. 1984. ≡ *Protostelium zonatum* L.S. Olive & Stoian., Amer. J. Bot 56(9): 985. 1969. Figs. 2c, 3g

Sporocarps. Sporocarps brownish to yellowish. Stalk 47-120 μ m long, beaded, having a chain-like appearance. Spore with a variable shape, from somewhat campanulate to elongated or irregular, $14.5\text{-}40.5 \times 24\text{-}46.5 \mu$ m, sometimes with warts that appear to be bacteria stuck to the spore surface. Prespore cells are slightly ellipsoid to round in outline (Spiegel & al., 2007).

Trophic stages. It grows and sporulates on various bacteria (e.g., Flavobacterium sp.) or on combinations of two food organisms such as Aureobasidium pullulans and a bacterium, or on two bacteria, according to preference of the particular isolate. Its trophic cells are nonpigmented, most frequently uninucleate but also plurinucleate, usually with a single large contractile vacuole. The amoebae are comparatively large, but they exhibit much variation in cell and nuclear size, and they can develop numerous filose pseudopodia in water. Plurinucleate protoplasts are not uncommon in some cultures, with their number of nuclei ranging from 2 to 16 or more. The cysts are very thin-walled, globose to subglobose or slightly irregular in outline, 22-40 µm diam. See Olive & al (1984).

It was originally described as *Protostelium zonatum* L.S. Olive & Stoian. (Olive & Stoianovitch, 1969). It is quite common worldwide and it is found frequently growing on substrates collected from a relatively dry habitat that is exposed to direct sunlight (Spiegel & al., 2007). It was rare but locally abundant in our cultures.

Specimens examined

Loc. 6: aerial litter of Fagus sylvatica, AS05-64. Loc. 16: aerial litter of Q. coccifera, GU06-07. Loc. 20: ground litter of Lavandula sp., M07-02; aerial litter of Q. ilex, M07-05; ground litter of Q. ilex, M07-06. Loc. 21: aerial litter of C. salvifolius, M07-13. Loc. 22: bark of Q. ilex, AV07-09. Loc. 23: aerial litter of R. sphaerocarpa, T007-03; bark of Q. ilex, T007-10. Loc. 24: aerial litter of Q. pyrenaica, AV07-13. Loc. 25: aerial litter of Q. ilex, T007-11. Loc. 26: bark of J. oxycedrus, GU07-09; bark of Q. ilex, GU07-10. Loc. 37: bark of Q. faginea, HU07-19. Loc. 45: ground litter of R. officinalis, NA07-30. Loc. 49: aerial litter of Gramineae, CU07-07. Loc. 58: ground litter of Gramineae, M06-16. Loc. 62: aerial litter of Epilobium hirsutum and Lithrum salicaria, O06-01. Loc. 74: ground litter of fern, GE08-16; aerial litter of Rosaceae, GE08-17. Loc. 85: aerial litter of Lavandula sp., P009-17.

7. *Microglomus paxillus L.S. Olive & Stoian., L.S. Olive & Stoian., J. Protozool. 24(4): 485. 1977. Figs. 2b, 3h

Sporocarps. Sporocarps 22.8-31.2 μm tall, with 2-4 spores. Stalk short, 9.6-16.8 μm long, tapering to form a thin tip. Spores are compressed against each other forming together an ellipsoidal structure slightly flattened in the upper side, 12-18.5 μm in diam., and can be observed through the sheath. Prespore cells are circular in outline (Olive & Stoianovitch, 1977b).

Trophic stages. It grows and sporulates on soft oak bark agar (at pH 6-6.6) or lactose-yeast extract agar (at pH 6), with a mixture of *Flavobacterium* sp. and *Dyadobacter* sp. strain Malaya. The amoebae are uninucleate and they usually have a single contractile vacuole. They have lobose pseudopodia with filose subpseudopodia. No flagellates have been ob-

served. The cysts are spherical to subspherical, $10.8-20.4 \mu m$ diam. See Olive & Stoianovitch (1977b).

It is an uncommon species worldwide (Spiegel & al., 2007), and it was very rarely found during present study.

Specimens examined

Loc. 2: bark of *Crataegus monogyna*, AS05-26. Loc. 12: bark of *Alnus* sp., AS05-115. Loc. 42: aerial litter of Gramineae, NA07-07. Loc. 61: ground litter of Leguminosae, M06-26.

8. Nematostelium gracile (L.S. Olive & Stoian.) L.S. Olive & Stoian., in Olive, Bot. Rev. 36(1): 68. 1970 [as gracilis].

≡ Schizoplasmodium gracile L.S. Olive & Stoian., J. Protozool. 13: 168. 1966 / Ceratiomyxella tahitiensis L.S. Olive & Stoian. Amer. J. Bot. 58(1): 32. 1971, complex

Figs. 2d, 3i

Two described species share this morphotype, but differ in details of ther life cycles. Studies on this complex must be carried out to clarify whether they are truly distinct (Spiegel & al., 2007).

Sporocarps. Stalks 42-240 μ m long, stiff, thick and robust, sometimes flexuous and waving in air currents, with a distinct knob-like apophysis present. Spores nearly spherical or apically flattened, 11.3-31.3 \times 13.8-33.8 μ m diam., deciduous. Prespore cells are round from above and hat-shaped from the side (Olive & Stoianovitch, 1971).

Trophic stages. N. gracile can be cultivated on wMY agar with mixtures of Kitani yeast with Dyadobacter sp. strain Malaya, or of Cryptococcus laurentii with Malaya bacterium. C. tahitiensis grows on malt-yeast extract agar or hay infusion agar (pH 6-7.3) with Dyadobacter sp. strain Malaya and the Kitani yeast at room temperature or in an incubator at 23 °C. They produce a thin, multinucleate, non-reticulate or reticulate plasmodium (Spiegel & Feldman, 1985). The plasmodium divides into irregular multinucleate masses before fruiting. C. tahitiensis in water produces anteriorly uniflagellate or occasionally bi-flagellate cells, with or without supernumerary flagella. N. gracile does not form flagellates. The cysts are round to irregular in outline. See Spiegel & Feldman (1986, 1991) for illustrations.

This species complex is very frequently found on samples. It is also common in temperate regions but it is almost absent at high latitudes, and above 2500 m (Spiegel & al., 2007). It was very common in our cultures. It has been previously recorded in Europe: in Germany (Tesmer & al., 2005) and in Russia (Kosheleva & al., 2009).

Specimens examined

Loc. 3: aerial litter of Lamiaceae, AS05-39. Loc. 13: aerial litter of Lavandula sp., M06-31; ground litter of Thymus sp., M06-34; aerial litter of Q. ilex, M06-35; aerial litter of G. scorpius, M06-37; ground litter of G. scorpius, M06-38. Loc. 14: aerial litter of R. sphaerocarpa, M06-43; ground litter of R. sphaerocarpa, M06-44. Loc. 15: ground litter of Gramineae, GU06-02; aerial litter of Lavandula sp., GU06-05; ground litter of Lavandula sp., GU06-06. Loc. 16: aerial litter of Q. coccifera, GU06-07; ground litter of Leguminosae, GU06-10. Loc. 17: aerial litter of R. officinalis, GU06-13; aerial litter of Q. coccifera, GU06-15; ground litter of Gramineae, CU06-01; aerial litter of thistle, CU06-03; ground litter of thistle, CU06-04. Loc. 19: aerial litter of Gramineae, CU06-05; ground litter of Gramineae, CU06-08. Loc. 20: ground litter of Lavandula sp., M07-02; aerial litter of Q. ilex, M07-05. Loc. 21: aerial litter of C. salvifolius, M07-13; ground litter of Lavandula sp., M07-18; bark of Q. ilex, M07-19. Loc. 22: bark of Q.

ilex, AV07-09. Loc. 23: aerial litter of O. ilex, TO07-01; ground litter of O. ilex, TO07-02; aerial litter of Lavandula sp., TO07-07; ground litter of Lavandula sp., TO07-08; bark of J. oxycedrus, TO07-09. Loc. 24: ground litter of C. ladanifer, AV07-12; bark of Q. pyrenaica, AV07-20. Loc. 25: aerial litter of thistle, TO07-13; ground litter of thistle, TO07-14; aerial litter of Lavandula sp., TO07-17; ground litter of Lavandula sp., TO07-18. Loc. 26: ground litter of Leguminosae, GU07-06. Loc. 32: aerial litter of Compositae, Z07-03. Loc. 35: aerial litter of Lygeum spartum, Z07-31; aerial litter of Arthrocnemum sp., Z07-33; ground litter of Arthrocnemum sp., Z07-34; aerial litter of Suaeda sp., Z07-36. Loc. 36: ground litter of Lygeum spartum, HU07-02; ground litter of Compositae, HU07-06; bark of J. phoenicea, HU07-10. Loc. 37: ground litter of Buxus sempervirens, HU07-12. Loc. 39: aerial litter of Fagus sylvatica, HU07-34; ground litter of Rosa sp., HU07-40. Loc. 41: ground litter of fern, HU07-54. Loc. 43: ground litter of Leguminosae, NA07-12; ground litter of Gramineae, NA07-15. Loc. 44: ground litter of Gramineae, NA07-22. Loc. 45: aerial litter of Gramineae, NA07-25; ground litter of Gramineae, NA07-26; ground litter of Cistaceae, NA07-28. Loc. 48: ground litter of Santolina sp., SO07-20. Loc. **49:** ground litter of *R. officinalis*, CU07-02; aerial litter of *Q. ilex*, CU07-03; aerial litter of Cistus albifolius, CU07-05; bark of Q. ilex, CU07-09; bark of J. oxycedrus, CU07-10. Loc. 50: ground litter of Compositae, CU07-14. Loc. 51: ground litter of Gramineae, CU07-28; bark of Pinus nigra, CU07-29. Loc. 52: ground litter of O. ilex, CU07-36; aerial litter of O. ilex, CU07-37. Loc. 53: ground litter of Lavandula sp., CU07-44; ground litter of Leguminosae, CU07-46. Loc. 54: aerial litter of Cistus sp., TE07-03; aerial litter of Cistus sp., TE07-04. Loc. 55: aerial litter of *Q. ilex*, TE07-09. Loc. 56: ground litter of *Retama* sphaerocarpa, M06-02. Loc. 57: ground litter of Leguminosae, M06-06; ground litter of Leguminosae, M06-12. Loc. 58: ground litter of Leguminosae, M06-14. Loc. 60: ground litter of Leguminosae, M06-22. Loc. 62: ground litter of Epilobium hirsutum and Lithrum salicaria, O06-02. Loc. 72: ground litter, SO06-04. Loc. 74: aerial litter of Castanea sativa, GE08-13; bark of Fagus sylvatica, GE08-20. Loc. 80: aerial litter of Cistus sp., BA09-21. Loc. 81: ground litter of Cistus sp., BA09-22; aerial litter of Leguminosae, BA09-24; ground litter of Lamiaceae, BA09-28. Loc. 83: ground litter of Cistus sp., H09-12. Loc. 92: aerial litter of Compositae, CO09-05; ground litter of Cistus sp., CO09-08.

Nematostelium ovatum (L.S. Olive & Stoian.) L.S. Olive & Stoian., in Olive, Bot. Rev. 36(1): 68. 1970.

 Schizoplasmodium ovatum L.S. Olive & Stoian., J. Protozool. 13: 164. 1966.

Sporocarps. Stalks 30-220 μ m long, thick and robust, with a distinct knob-like apophysis. Spores ovoid to ellipsoid, 10-18.5 \times 13-29 μ m in diam., deciduous, that have a distinct ring-shaped hilum with a raised edge that fits with the apophysis of the stalk. Prespore cells round from above and hat-shaped from the side.

Trophic stages. It grows on wMY agar on Flavobacterium sp or with mixtures of Kitani yeast with Dyadobacter sp. strain Malaya, or of Cryptococcus larentii with Dyadobacter sp. strain Malaya. When spores germinate, they produce a thin, multinucleate, branching to reticulate plasmodium, that divides into irregular multinucleate masses before fruiting. The cysts are round to irregular in shape. See Olive & Stoianovitch, (1966c).

This species was originally described as *Schizoplasmodium ovatum* L.S. Olive & Stoian.. It is quite common in temperate areas, and less frequent but also abundant in tropical localities (Spiegel & al., 2007). It was locally common in the Iberian Peninsula. In Europe, this species has been previously recorded in Germany (Tesmer & al., 2005) and Russia (Kosheleva & al., 2009).

Specimens examined

Loc. 6: ground litter of *Fagus sylvatica*, AS05-65. **Loc. 10:** ground litter of *Tilia* sp., AS05-94. **Loc. 13:** aerial litter of *Lavandula* sp., M06-31. **Loc. 16:** ground litter of Leguminosae, GU06-10. **Loc. 17:** aerial litter of Gramineae,

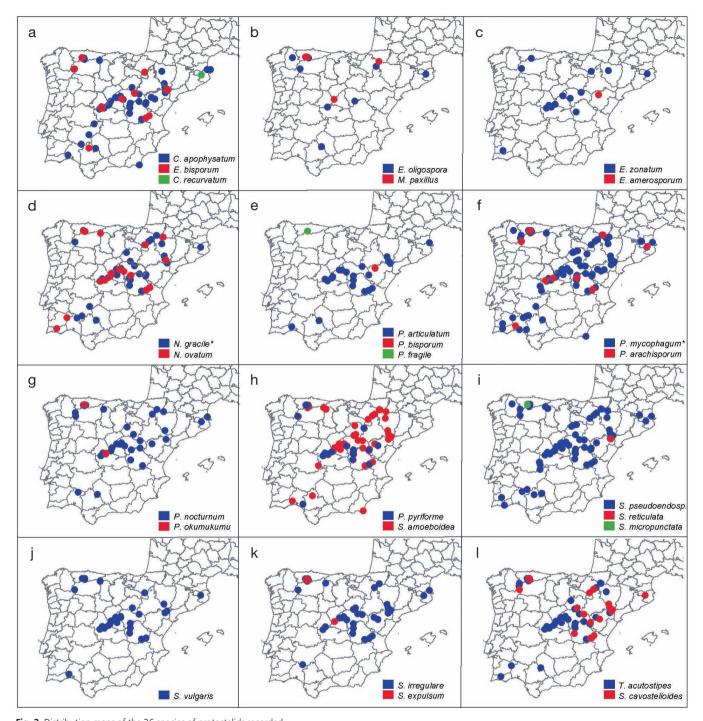


Fig. 2. Distribution maps of the 26 species of protostelids recorded.

GU06-11; aerial litter of *R. officinalis*, GU06-13; ground litter of *Q. coccifera*, GU06-16. Loc. 20: ground litter of *Lavandula* sp., M07-02. Loc. 23: ground litter of *Q. ilex*, TO07-02. Loc. 25: aerial litter of *Lavandula* sp., TO07-17. Loc. 34: bark of *Juniperus* sp., Z07-23. Loc. 39: ground litter of *F. sylvatica*, HU07-32; ground litter of *Quercus* sp., HU07-33. Loc. 45: ground litter of Gramineae, NA07-26. Loc. 51: bark of *Pinus nigra*, CU07-29. Loc. 52: aerial litter of *Q. coccifera*, CU07-31. Loc. 60: ground litter of Leguminosae, M06-22. Loc. 66: ground litter of Leguminosae, EE06-04. Loc. 84: ground litter of *Q. ilex*, PO09-04. Loc. 86: ground litter of *Q. suber*, PO09-28.

10. Protosporangium articulatum L.S. Olive & Stoian., J. Protozool. 19(4): 570. 1972. Figs. 2e, 3k

Sporocarps. Multispored sporocarps, 80-185 µm tall. Stalk proportionally very long and flexuous, with an articulation near the point of attachment to the spore, that bends in air currents. They have spherical to ellipsoid structures, formed by hemispherical spores, $5\text{-}7.5\times6.3\text{-}10~\mu\text{m}$, connected by their flat surfaces. The spores are uninucleate and nondeciduous. Prespore cells are circular in outline (Olive & Stoianovitch, 1972).

Trophic stages. It can be cultivated on maltose-yeast extract agar (pH 5.1-5.8) with Malaya-82 or on oak bark agar. The

spores give rise to flagellate cells immediately after germination, $11.3-27 \times 13.8-35$ µm. The flagella usually occur in pairs (1 long and 1 short). The amoeboid cells have 1 or a few nuclei, but up to 21 nuclei have been observed within a single cell. The amoebae are flattened or slightly raised, and circular to elliptical in outline (Spiegel & Feldman, 1985). They do not return to the flagellate stage when placed in water. It has also been observed a vermiform stage, but it is less common than in other members of the genus. The cysts contain 1-5 nuclei, and are globose to oval or occasionally irregular. See Spiegel & Feldman (1984) and Spiegel & al. (1986) for illustrations.

Our material shows sporocarps bearing two spores in most cases, but also four-spored sporocarps were observed. They grow frequently on bark and wood. It appears to be a species that is often associated with arid habitats, and it occurs at higher elevations (>3000m) than most protostelids (Spiegel & al., 2007). It was fairly common in our cultures. In Europe, it was previously found in Russia (Kosheleva & al., 2009), France, and England (Olive, 1975).

Specimens examined

Loc. 13: aerial litter of *Thymus* sp., M06-33; aerial litter of *Q. ilex*, M06-35; ground litter of G. scorpius, M06-38. Loc. 16: aerial litter of Leguminosae. GU06-09. Loc. 17: aerial litter of R. officinalis, GU06-13; aerial litter of Q. coccifera, GU06-15. Loc. 19: ground litter of Gramineae, CU06-06; aerial litter of Thymus sp., CU06-07. Loc. 20: aerial litter of Lavandula sp., M07-01; aerial litter of Q. ilex, M07-05. Loc. 21: aerial litter of Q. ilex, M07-11; aerial litter of C. salvifolius, M07-13; aerial litter of Lavandula sp., M07-17. Loc. 23: ground litter of J. oxycedrus, TO07-06. Loc. 24: bark of Q. pyrenaica, AV07-20. Loc. 27: bark of Juniperus sp., GU07-16. Loc. 32: bark of J. phoenicea, Z07-09. Loc. 34: bark of P. halepensis, Z07-24; aerial litter of P. halepensis, Z07-27. Loc. 36: bark of J. phoenicea, HU07-10. Loc. 49: aerial litter of R. officinalis, CU07-01; aerial litter of Cistus albifolius, CU07-05. Loc. 50: ground litter of Q. ilex, CU07-16. Loc. 51: aerial litter of Leguminosae, CU07-21; aerial litter of Gramineae, CU07-27; ground litter of Gramineae, CU07-28; bark of Pinus nigra, CU07-29; bark of Juniperus sp., CU07-30. Loc. 52: aerial litter of Q. coccifera, CU07-31; aerial litter of Q. ilex, CU07-37; ground litter of Leguminosae, CU07-38. Loc. 54: aerial litter of Cistus sp., TE07-03. Loc. 57: aerial litter of Leguminosae, M06-05; ground litter of Gramineae, M06-08. Loc. 73: ground litter of Erica sp., GE08-04; aerial litter of Acer monspessulanum, GE08- 07. Loc. 87: ground litter of Q. ilex, H09-21. Loc. 92: aerial litter of Cistus sp., CO09-07.

11. *Protosporangium bisporum L.S. Olive & Stoian., J. Protozool. 19(4): 565. 1972. Fig. 2e

Sporocarps. Sporocarps 90-220 μ m tall. Sporangia globose, 10-13.8 μ m in diam., with 1 or 2 spores. Stalks very long, thin and flexuous. Spores hemispherical, 5-7 \times 10-13.8 μ m, non-deciduous. Prespore cells circular in outline.

Trophic stages. It grows and sporulates on oak bark agar (pH 8), with *Dyadobacter* sp. strain Malaya bacterium and a moniliaceous fungus (*Goetricum* sp.). The fungus is generally necessary for sporulation, but it may also sporulate in the vicinity of *Penicillium* sp. Single spores give rise to 8 flagellate cells on germination, while spores in pairs produce 4 flagellate cells. Flagellate cells typically have a single anterior flagellum, but occasionally two of equal length are present, and only rarely it is possible to find a short flagellum paired with the longer one. Pseudoflagella (ephemeral filose extensions of the flagellate cell) are commonly seen. Plurinucleate protoplasts that do not develop flagella or become reticulate may be found in cultures several days after spore germination.

Protoplasmodia divide by plasmotomy, which tends to limit their size and nuclear number. Under certain conditions, the plurinuceate protoplasts become converted into worm-like structures. This vermiform phase has an almost segmented appearance, and undulates changing the shape of the swellings constantly. At one or both ends of the protoplast there are knob-like areas with short filose pseudopodia. Cysts round to oval or somewhat irregular, 16.3-33.8 × 22.5-53.8 µm. See Olive & Stoianovitch (1972).

This is a very uncommon species and it is usually found on bark of living trees, sometimes forming dense patches (Spiegel & al., 2007), and it was found only once during this study.

Specimens examined

Loc. 28: aerial litter of Lamiaceae, TE07-19.

12. *Protosporangium fragile L.S. Olive & Stoian., J. Protozool. 19(4): 568. 1972. Figs. 2e, 3l

Sporocarps. Sporocarps 65-225 μ m tall, that move in air currents. Stalk proportionally long, flexuous and easily fragmented. Spores, 4.3- 5.5×5.3 - 7.5μ m, in groups of four, forming structures, 7.5-11 in diam. (Olive & Stoianovitch, 1972). Prespore cells unknown.

Trophic stages. It grows on malt-yeast extract agar with an unidentified bacterium, isolated from hickory bark, as its food source. The species has a restricted pH tolerance in culture and fails to grow if the pH deviates significantly from 5.1. Each spore germinates giving rise to 2 flagellate cells. The trophic stage consists of uninucleate or plurinucleate ameboid cells, that can produce filose pseudopodia when the cells are placed in water. They can also form a vermiform stage, readily reversible to the flattened ameboid phase. The flagellate cells commonly have either 1 long anterior flagellum, paired with a short reflexed one, or a pair of long flagella. The short flagellum tends to lie against the side of the cell and usually is inconspicuous. Pseudoflagella commonly appear at the apical end of the cell and migrate to the posterior end where they disappear. The nucleus, containing a small central nucleolus, is situated in the more or less hyaloplasmic anterior 1/3 of the cell. The cysts are globose, oval, oblong, or occasionally irregular, $10-27 \times 13.8-35 \mu m$. See Olive & Stoianovitch (1972).

It is an uncommon species found in most cases growing on bark of living trees or on rotting wood (Spiegel & al., 2007), and it was found only once during this study.

Specimens examined

Loc. 2: bark of Crataegus monogyna, AS05-26.

13. "Protostelium" arachisporum L.S. Olive, Amer. J. Bot 49(3): 301. 1962. Figs. 2f, 3m

Sporocarps. Stalk relatively long, 19.5-62.5 μ m, narrow, with a small knob-like apophysis. Spores very variable in shape, from almost spherical or ovate to elongate with one or more constrictions resembling the pod of a peanut, 8.8-9.3 \times 20-46 μ m. Prespore cells slightly ellipsoid to round in outline (Olive, 1962).

Trophic stages. It grows on lactose-yeast or wMY agar, with Flavobacterium sp.. The fanshaped amoebae have filose sub-pseudopodia and a single distinct nucleus. They present a

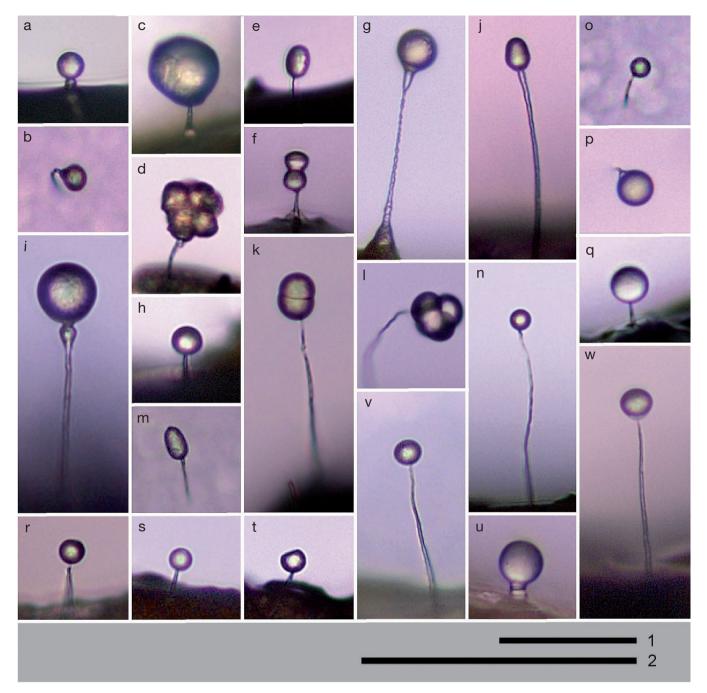


Fig. 3. Fruiting bodies of protostelids: **a,** Cavostelium apophysatum; **b,** Clastostelium recurvatum; **c, d,** Echinosteliopsis oligospora; **e, f,** Echinostelium bisporum; **g,** Endostelium zonatum; **h,** Microglomus paxillus; **i,** Nematostelium gracile / Ceratiomyxella tahitiensis; **j,** Nematostelium ovatum; **k,** Protosporangium articulatum; **l,** Protosporangium fragile; **m,** Protostelium arachisporum; **n,** Protostelium mycophagum / Planoprotostelium aurantium; **o,** Protostelium nocturnum; **p,** Protostelium pyriforme; **q,** Schizoplasmodiopsis amoeboidea; **r,** Schizoplasmodiopsis micropunctata; **s,** Schizoplasmodiopsis pseudoendospora; **t,** Schizoplasmodiopsis vulgaris; **u,** Schizoplasmodium cavostelioides; **v,** Soliformovum irregulare; **w,** Tychosporium acutostipes. Bars 50 µm; 1 for a-h, j-w, and 2 for i.

contractile vacuole, and a scalloped, hyaline anterior border when migrating across the agar surface. The microcysts are spherical and thin-walled, 10-2.8 µm diam. See Olive (1962).

This fairly common species is more abundant in the tropics than in temperate areas. It probably represents a species complex and is unlikely to be a member of the eumycetozoans (Spiegel & al., 2007). It was quite uncommon in our cultures, and it has been previously recorded in Europe in Germany

(Tesmer & al., 2005) and Russia (Kosheleva & al., 2009). This species has been excluded from the genus *Protostelium* (Spiegel & al., 1994), but has yet to be assigned a new genus (see Table 1).

Specimens examined

Loc. 10: bark of *Pinus sylvestris*, AS05-95. Loc. 19: aerial litter of Gramineae, CU06-05. Loc. 21: ground litter of *Quercus ilex*, M07-12. Loc. 25:

bark of *Quercus ilex*, TO07-20. **Loc. 41:** ground litter of fern, HU07-54. **Loc. 51:** aerial litter of Leguminosae, CU07-21. **Loc. 62:** aerial litter of *Epilobium hirsutum* and *Lithrum salicaria*, O06-01. **Loc. 74:** ground litter of Castanea sativa, GE08-14; bark of *Quercus* sp., GE08-19. **Loc. 87:** bark of *Q. ilex*, H09-29

14. Protostelium mycophagum L.S. Olive & Stoian., Bull. Torrey Bot. Club 87(1): 12. 1960 [as *mycophaga*] / **Planoprotostelium aurantium** L.S. Olive & Stoian., J. Elisha Mitchell Sci. Soc. 87(3): 115. 1971, **complex**.

Figs. 2f, 3n

Sporocarps. Most individuals have sporocarps that move easily in air currents, others have piliform sections in their stalks that float and curl continuously, even in the absence of evident air currents, while others present stiffer stalks. Stalks less than 70 µm long, tapered at maturity, flexuous, and flexible, often presenting a small apophysis at their tips. Spores spherical to slightly obpyriform, 8.8-13.8 µm in diam., smooth (Olive & Stoianovitch, 1969). Prespore cells are elliptical when viewed from above.

Trophic stages. The amoebae are reported to feed upon bacteria (Flavobacterium sp. and Aerobacter aerogenes) as well as fungi, Rhodotorula mucilaginosa and Cryptococcus laurentii (Olive & Stoianovitch, 1969). However, according to F.W. Spiegel (personal communication) many strains will not fruit if any bacteria are present in culture. They are uninucleate, with a prominent nucleolus in interphase. Amoebae contain one to three prominent contractile vacuoles and numerous pink to orange lipid droplets. Migrating amoebae produce broad, lamellate pseudopodia, with some blunt to acutely pointed subseudopodia extending from them. More elongated, pointed subpseudopodia are found under wetter conditions. The shape of the amoebae varies from irregularly circular to elongate to occasionally flabellate. Amoebae may move by the gently eruptive production of pseudopodia that subsequently appear to pull the cell along, or they may glide along the substratum. Gliding is faster than pseudopodial crawling. They have distinct three-dimensional relief when viewed on the surface of a culture plate (Spiegel & al., 1994).

This species is very variable in its morphology, both in size and deciduousness of spores, and probably constitutes a species complex (Spiegel & al., 2007). This is one of the most frequently encountered species worldwide (Spiegel & al., 2007), and in this study. In Europe, this species has been reported from Holland (Olive, 1962, 1967), Sweden (Olive, 1962, 1967), Greece (Olive, 1967), Germany (Tesmer & al., 2005) and Russia (Kosheleva & al., 2009).

Specimens examined

Loc. 1: aerial litter of *Pteridium aquilinum*, AS05-5; ground litter of *Pteridium aquilinum*, AS05-6; aerial litter of Compositae, AS05-11; ground litter of Compositae, AS05-12. Loc. 2: aerial litter of *Cytisus* sp., AS05-20; ground litter of thistle, AS05-23; ground litter of *Crataegus monogyna*, AS05-25. Loc. 3: ground litter of *Cytisus* sp., AS05-32; aerial litter of *Hedera helix*, AS05-35; aerial litter of Lamiaceae, AS05-39. Loc. 4: aerial litter of *Erica* sp., AS05-48; aerial litter of *Mentha* sp., AS05-52; ground litter of *Mentha* sp., AS05-52. Loc. 5: aerial litter of *Crytus avellana*, AS05-62. Loc. 6: aerial litter of *Fagus sylvatica*, AS05-64. Loc. 9: aerial litter of Lamiaceae, AS05-81; aerial litter of Lamiaceae, AS05-82; aerial litter of *Cytisus* sp., AS05-83. Loc. 10: aerial litter of Poaceae, AS05-87; aerial litter of *Aesculus hippocastanum*, AS05-88; bark of *Pinus sylvestris*, AS05-95. Loc. 11: aerial litter of *Rubus* sp., AS05-96; ground litter of *Campanula* sp., AS05-101; aerial litter of Compositae, AS05-96; ground litter of *Campanula* sp., AS05-101; aerial litter of Compositae, AS05-

102; ground litter of Compositae, AS05-103; aerial litter of Tilia sp., AS05-104. Loc. 12: aerial litter of *Rubus* sp., AS05-109; ground litter of *Rubus* sp., AS05-110; aerial litter Lamiaceae, AS05-111; aerial litter of Alnus sp., AS05-113; ground litter of Cyperaceae, AS05-117; ground litter of Rumex sp., AS05-118; ground litter of Equisetum sp., AS-121. Loc. 13: aerial litter of Gramineae, M06-29; ground litter of Gramineae, M06-30; aerial litter of Lavandula sp., M06-31; ground litter of Lavandula sp., M06-32; aerial litter of Thymus sp., M06-33; ground litter of Thymus sp., M06-34; aerial litter of O. ilex, M06-35; ground litter of G. scorpius, M06-38, Loc. 14; aerial litter of C. ladanifer, M06-39; ground litter of C. ladanifer, M06-40; aerial litter of Gramineae, M06-41; ground litter of Gramineae, M06-42; aerial litter of R. sphaerocarpa, M06-43. Loc. 15: aerial litter of Gramineae, GU06-01; ground litter of Gramineae, GU06-02; aerial litter of Leguminosae, GU06-03; ground litter of Leguminosae, GU06-04; aerial litter of Lavandula sp., GU06-05; ground litter of Lavandula sp., GU06-06. Loc. 16: aerial litter of Q. coccifera, GU06-07; ground litter of Q. coccifera, GU06-08; aerial litter of Leguminosae, GU06-09. Loc. 17: aerial litter of Gramineae, GU06-11; ground litter of Gramineae, GU06-12; aerial litter of R. officinalis, GU06-13; ground litter of R. officinalis, GU06-14; aerial litter of Q. coccifera, GU06-15. Loc. 18: aerial litter of Gramineae, CU06-01; ground litter of Gramineae, CU06-02; aerial litter of thistle, CU06-03; ground litter of thistle CU06-04. Loc. 19: aerial litter of Gramineae, CU06-05; ground litter of Gramineae, CU06-06; aerial litter of Thymus sp., CU06-07; ground litter of Thymus sp., CU06-08. Loc. 20: aerial litter of Lavandula sp., M07-01; ground litter of Lavandula sp., M07-02; aerial litter of R. sphaerocarpa, M07-03; ground litter of R. sphaerocarpa, M07-04; aerial litter of *Q. ilex*, M07-05; aerial litter of Gramineae, M07-07; ground litter of Gramineae, M07-08. Loc. 21: aerial litter of Q. ilex, M07-11; aerial litter of C. salvifolius, M07-13; ground litter of C. salvifolius, M07-14; aerial litter of Gramineae, M07-15; aerial litter of Lavandula sp., M07-17; ground litter of Lavandula sp., M07-18. Loc. 22: aerial litter of Leguminosae, AV07-01; ground litter of Leguminosae, AV07-02; aerial litter of O. ilex, AV07-03; aerial litter of Gramineae, AV07-05. Loc. 23: aerial litter of Q. ilex, TO07-01; aerial litter of R. sphaerocarpa, TO07-03; ground litter of R. sphaerocarpa, TO07-04; aerial litter of *J. oxycedrus*, TO07-05; ground litter of *J. oxycedrus*, TO07-06; aerial litter of Lavandula sp., TO07-07; bark of Q. ilex, TO07-10. Loc. 24: aerial litter of C. ladanifer, AV07-11; aerial litter of Q. pyrenaica, AV07-13; ground litter of Quercus pyrenaica, AV07-14; aerial litter of Rubus sp., AV07-15; ground litter of *Rubus* sp., AV07-16. Loc. 25: aerial litter of *Q.* ilex, TO07-11; aerial litter of thistle, TO07-13; ground litter of thistle, TO07-14; ground litter of C. ladanifer, TO07-16; aerial litter of Lavandula sp., TO07-17; bark of Q. ilex, TO07-20. Loc. 26: aerial litter of Gramineae, GU07-01; ground litter of Gramineae, GU07-02; aerial litter of Santolina sp., GU07-03; ground litter of Santolina sp., GU07-04; aerial litter of Leguminosae, GU07-05; aerial litter of Thymus sp., GU07-07; bark of J. oxycedrus, GU07-09. Loc. 27: aerial litter of Juniperus thurifera, GU07-13; aerial litter of Lavandula sp., GU07-15; bark of Juniperus sp., GU07-16; aerial litter of Leguminosae, GU07-17; ground litter of Leguminosae, GU07-18; bark of Ulmus sp., GU07-20. Loc. 28: aerial litter of Lamiaceae, TE07-19; ground litter of Lamiaceae, TE07-20; aerial litter of Q. faginea, TE07-25; bark of Q. faginea, TE07-27. Loc. 29: aerial litter of Erinacea anthyllis, TE07-28; aerial litter of Lamiaceae, TE07-30; ground litter of Gramineae, TE07-33; aerial litter of Brassicaceae, TE07-34. Loc. 30: aerial litter of Compositae, TE07-38; ground litter of Leguminosae, TE07-41. Loc. 31: aerial litter of Lamiaceae, TE07-45; aerial litter of Cistaceae, TE07-47; ground litter of Cistaceae, TE07-48; aerial litter of Gramineae, TE07-49. Loc. 32: aerial litter of R. officinalis, Z07-01; aerial litter of Compositae, Z07-03; aerial litter of Gramineae, Z07-05. Loc. 33: ground litter of Gramineae, Z07-14; bark of Pinus halepensis, Z07-16; aerial litter of Pistacia lentiscus, Z07-19. Loc. 34: bark of Juniperus sp., Z07-23; aerial litter of Gramineae, Z07-25; aerial litter of P. halepensis, Z07-27. Loc. 35: aerial litter of Lygeum spartum, Z07-31; aerial litter of Arthrocnemum sp., Z07-33; aerial litter of Suaeda sp., Z07-35; aerial litter of Salsola sp., Z07-37. Loc. 36: aerial litter of Lygeum spartum, HU07-01; ground litter of Lygeum spartum, HU07-02; aerial litter of Lamiaceae, HU07-03; aerial litter of Compositae, HU07-05; ground litter of Compositae, HU07-06; bark of J. phoenicea, HU07-10. Loc. 37: aerial litter of Buxus sempervirens, HU07-11; aerial litter of *Ulex* sp., HU07-13; aerial litter of Gramineae, HU07-15; ground litter of Gramineae, HU07-16; aerial litter of Arctostaphyllos uva-ursi, HU07-18; bark of Q. faginea, HU07-19. Loc. 38: bark of Salix sp., HU07-23; aerial litter of Geum sp., HU07-27; ground litter of Geum sp., HU07-28. Loc. 39: aerial litter of Populus tremula, HU07-35; aerial litter of Rosa sp., HU07-39. Loc. 40: aerial litter of Gramineae, HU07-41; ground litter of Buxus sem-

pervirens, HU07-44; aerial litter of Leguminosae, HU07-47. Loc. 41: ground litter of F. sylvatica, HU07-52; aerial litter of fern, HU07-53; ground litter of fern, HU07-54. Loc. 42: aerial litter of F. sylvatica, NA07-03; aerial litter of P. sylvestris, NA07-05; aerial litter of Gramineae, NA07-07; ground litter of Gramineae, NA07-08. Loc. 43: aerial litter of Q. humilis, NA07-09; ground litter of O. humilis, NA07-10; aerial litter of Leguminosae, NA07-11; aerial litter of Gramineae, NA07-13; ground litter of Gramineae, NA07-15. Loc. 44: aerial litter of B. sempervirens, NA07-17; aerial litter of Q. coccifera, NA07-19; ground litter of O. coccifera, NA07-20; aerial litter of Gramineae, NA07-21. Loc. 45: aerial litter of Leguminosae, NA07-23; aerial litter of Gramineae, NA07-25; ground litter of Gramineae, NA07-26; aerial litter of Cistaceae, NA07-27; aerial litter of *R. officinalis*, NA07-29; ground litter of Compositae, NA07-32; aerial litter of *Atriplex halimus*, NA07-33. **Loc. 46:** aerial litter of *Q.* pyrenaica, SO07-01; aerial litter of J. communis, SO07-03; ground litter of Gramineae, SO07-06; aerial litter of *Q. ilex*, SO07-07; ground litter of *Q. ilex*, SO07-08. Loc. 47: aerial litter of Lamiaceae, SO07-09; ground litter of Gramineae, SO07-14; ground litter of Leguminosae, SO07-16. Loc. 48: ground litter of Lamiaceae, SO07-18; aerial litter of Santolina sp., SO07-19; ground litter of Santolina sp., SO07-20; aerial litter of Gramineae, SO07-22. Loc. 49: aerial litter of R. officinalis, CU07-01; aerial litter of Cistus albifolius, CU07-05; ground litter of Cistus albifolius, CU07-06; aerial litter of Gramineae, CU07-07; ground litter of Gramineae, CU07-08; bark of *I. oxyce*drus, CU07-10. Loc. 50: aerial litter of Thymus sp., CU07-11; aerial litter of Compositae, CU07-13; ground litter of Compositae, CU07-14; aerial litter of Q. ilex, CU07-15; ground litter of Q. ilex, CU07-16; ground litter of Gramineae, CU07-18; bark of Pinus sp., CU07-20. Loc. 51: ground litter of Leguminosae, CU07-22; aerial litter of Thymus sp., CU07-23; ground litter of Thymus sp., CU07-24; aerial litter of R. officinalis, CU07-25; ground litter of R. officinalis, CU07-26; aerial litter of Gramineae, CU07-27; ground litter of Gramineae, CU07-28; bark of Pinus nigra, CU07-29; bark of Juniperus sp., CU07-30. Loc. 52: aerial litter of *Q. coccifera*, CU07-31; aerial litter of *Q. ilex*, CU07-35; ground litter of Q. ilex, CU07-36; aerial litter of Q. ilex, CU07-37; ground litter of Leguminosae, CU07-38. Loc. 53: aerial litter of Thymus sp., CU07-41; ground litter of Thymus sp., CU07-42; aerial litter of Lavandula sp., CU07-43; ground litter of Lavandula sp., CU07-44; aerial litter of Leguminosae, CU07-45; ground litter of Gramineae, CU07-48. Loc. 54; aerial litter of J. communis, TE07-01; aerial litter of Cistus sp., TE07-04; aerial litter of Rosaceae, TE07-06. Loc. 55: aerial litter of Q. ilex, TE07-09; ground litter of O. ilex, TE07-10; aerial litter of Cistus sp., TE07-11; bark of O. ilex, TE07-17. Loc. 56: aerial litter of Retama sphaerocarpa, M06-01; ground litter of Retama sphaerocarpa, M06-02; ground litter of Gramineae, M06-04. Loc. 57: aerial litter of Leguminosae, M06-05; aerial litter of Gramineae, M06-07; ground litter of Gramineae, M06-08; aerial litter of Leguminosae, M06-09; aerial litter of Leguminosae, M06-11; ground litter of Leguminosae, M06-12. Loc. 58: aerial litter of Leguminosae, M06-13; ground litter of Leguminosae, M06-14; ground litter of Gramineae, M06-16. Loc. 59: ground litter of Leguminosae, M06-18. Loc. 60: aerial litter of Leguminosae, M06-21; ground litter of Leguminosae, M06-22; ground litter of Gramineae, M06-24. Loc. 61: aerial litter of Leguminosae, M06-25; ground litter of Leguminosae, M06-26. Loc. 62: aerial litter of Epilobium hirsutum and Lithrum salicaria, O06-01; ground litter of Epilobium hirsutum and Lithrum salicaria, O06-02. Loc. 63: aerial litter of Gramineae, LE06-01. Loc. 64: aerial litter of Leguminosae, LU06-01. Loc. 65: aerial litter of Chamaespartium tridentatum, LU06-03. Loc. 66: aerial litter of Leguminosae, LE06-03; ground litter of Leguminosae, LE06-04. Loc.68: ground litter, AL07-02. Loc. 69: ground litter, SO06-01. Loc. 71: ground litter, SO06-03. Loc. 72: ground litter, SO06-04. Loc. 73: aerial litter of Erica sp., GE08-03; ground litter of Erica sp., GE08-04; aerial litter of Quercus suber, GE08-05; ground litter of Quercus suber, GE08-06; aerial litter of Acer monspessulanum, GE08-07. Loc. 74: aerial litter of Fagus sylvatica, GE08-11; ground litter of Fagus sylvatica, GE08-12; aerial litter of Castanea sativa, GE08-13; aerial litter of Rosaceae, GE08-17; ground litter of Rosaceae, GE08-18. Loc. 75: bark of Q. ilex, CA09-09. Loc. 77: ground litter of Gramineae, CA09-24. Loc. 80: aerial litter of Gramineae, BA09-11; aerial litter of Leguminosae, BA09-15; aerial litter of Cistus sp., BA09-21. Loc. 81: aerial litter of Leguminosae, BA09-24; aerial litter of Gramineae, BA09-25; ground litter of Gramineae, BA09-26; aerial litter of Lamiaceae, BA09-27. Loc. 82: aerial litter of Lamiaceae, H09-07. Loc. 83: ground litter of Cistus sp., H09-12; aerial litter of Q. suber, H09-17. Loc. 84: aerial litter of Gramineae, PO09-01; ground litter of Gramineae, PO09-02. Loc. 85: aerial litter of Cistus sp., PO09-11. Loc. 86: aerial litter of Cistus sp., PO09-21; aerial litter of Q. ilex, PO09-27. Loc. 88: bark, H09-33. Loc. 89: ground litter, H09-35. Loc. 92: aerial litter of Gramineae, CO09-01; ground litter of Gramineae, CO09-02; aerial litter of *Q. ilex*, CO09-03; aerial litter of Compositae, CO09-05; ground litter of Compositae, CO09-06; aerial litter of *Cistus* sp., CO09-07. Loc. 96: ground litter of thistle, FR08-02; aerial litter of Gramineae, FR08-03; ground litter of gramineae, FR08-04; ground litter of Compositae, FR08-06; aerial litter of Rosaceae, FR08-07; ground litter of Compositae, FR08-10. Loc. 97: aerial litter of *Betula* sp., FR08-17.

15. Protostelium nocturnum Spiegel, Mycologia 76(3): 443. 1984. Figs. 2g, 3o

Sporocarps. Sporocarps similar in shape to those of *P. my-cophaga*, but smaller in size. Stalk (15.6)18-26(31.2) μm long. Spores nearly spherical, (6.5)7.5-10.4 μm in diam., smooth, soon actively released with the disappearance of the stalk (Spiegel, 1984). Prespore cells are elliptical.

Trophic stages. It grows on wMY agar or hay infusion agar with Xanthomonas fragariae (Fla-20 isolate of Olive) or Rhodotorula mucilaginosa, and on CM+ agar with Rhodotorula. It grows well but fruits poorly on CM+ with X. fragariae. The amoebae are small, uninucleate, with a single central nucleolus, and one or more contractile vacuoles and many food vacuoles. Orange pigmented lipid droplets are also present. They are relatively smooth in outline on dry agar, but acutely pointed pseudopodia and lamellopodia become increasingly prominent as the medium becomes more liquid. The microcysts are spherical or ellipsoidal. See Spiegel (1984).

This species fruit most heavily after sunset until early morning. It is relatively common worldwide (Spiegel & al., 2007) and also common in the Iberian Peninsula. This species has been previously cited in Europe for Germany (Tesmer & al., 2005).

Specimens examined

Loc. 1: aerial litter of Pteridium aquilinum, AS05-5. Loc. 2: ground litter of thistle, AS05-23. Loc. 3: ground litter of Cytisus sp., AS05-32; ground litter of Hedera helix, AS05-36. Loc. 10: ground litter of Tilia sp., AS05-94. Loc. 11: aerial litter of Rubus sp., AS05-96; ground litter of Campanula sp., AS05-101; aerial litter of Compositae, AS05-102; ground litter of Compositae, AS05-103; aerial litter of Tilia sp., AS05-104. Loc. 12: aerial litter of Lamiaceae, AS05-111. Loc. 13: ground litter of Gramineae, M06-30; aerial litter of Lavandula sp., M06-31; aerial litter of Thymus sp., M06-33; ground litter of G. scorpius, M06-38. Loc. 14: aerial litter of C. ladanifer, M06-39; aerial litter of Gramineae, M06-41; aerial litter of R. sphaerocarpa, M06-43. Loc. 15: aerial litter of Lavandula sp., GU06-05. Loc. 16: aerial litter of Leguminosae, GU06-09. Loc. 17: aerial litter of R. officinalis, GU06-13; aerial litter of Q. coccifera, GU06-15. Loc. 20: aerial litter of Q. ilex, M07-05. Loc. 22: aerial litter of Q. ilex, AV07-03. Loc. 24: aerial litter of Q. pyrenaica, AV07-13; ground litter of Quercus pyrenaica, AV07-14; ground litter of Rubus sp., AV07-16. Loc. 25: aerial litter of Q. ilex, TO07-11. Loc. 27: aerial litter of Lavandula sp., GU07-15. Loc. 28: aerial litter of Lamiaceae, TE07-19; bark of Q. faginea, TE07-27. Loc. 31: ground litter of Cistaceae, TE07-48; aerial litter of Gramineae, TE07-49. Loc. 36: aerial litter of Lygeum spartum, HU07-01. Loc. 39: aerial litter of Fagus sylvatica, HU07-34. Loc. 42: aerial litter of Rosa sp., NA07-01. Loc. 43: aerial litter of Q. coccifera, NA07-16. Loc. 47: aerial litter of Lamiaceae, SO07-09. Loc. 49: aerial litter of R. officinalis, CU07-01; aerial litter of Cistus albifolius, CU07-05. Loc. 50: aerial litter of Q. ilex, CU07-15. Loc. 53: aerial litter of Lavandula sp., CU07-43. Loc. 58: ground litter of Leguminosae, M06-14. Loc. 59: ground litter of Leguminosae, M06-18. Loc. 60: ground litter of Leguminosae, M06-22. Loc. 61: ground litter of Leguminosae, M06-26. Loc. **62:** aerial litter of *Epilobium hirsutum* and *Lithrum salicaria*, O06-01; ground litter of Epilobium hirsutum and Lithrum salicaria, O06-02. Loc. 63: aerial litter of Gramineae, LE06-01. Loc. 67: ground litter of Leguminosae, PA06-02. Loc. 72: ground litter, SO06-04. Loc. 73: aerial litter of Erica sp., GE08-03; ground litter of Erica sp., GE08-04. Loc. 74: aerial litter of Fagus sylvatica, GE08-11; aerial litter of Castanea sativa, GE08-13; aerial litter of Rosaceae, GE08-17. Loc. 83: aerial litter of Gramineae, H09-15. Loc. 92: ground litter of *Cistus* sp., CO09-08.

16. *Protostelium okumukumu Spiegel, Shadwick & Hemmes, Mycologia 98(1): 151. 2006. Fig. 2g

Sporocarps. Sporocarps 15-25 μ m tall, ballistosporous. Stalk bipartite, with two segments separated by an articulation, apophysis spherical to ovoid present. Spore nearly spherical, (7.2)9.5-10.5 μ m in diam. When intact, the spore and the apophysis flag at the articulation point. The spore is actively shot with the disappearance of the apophysis and only the rigid basal portion of the stalk remains, resembling "beard stubble". Prespore cells are elliptical (Spiegel & al., 2006).

Trophic stages. It can be cultivated on wMY agar at 20-24 °C with the yeast *Cryptococcus laurentii* or *Rhodotorula mucilaginosa*. The spores liberate the uninucleate, nonflagellated amoebae typical of the genus *Protostelium*, sensu Spiegel & al. (1994). The amoebae contain light orange lipid droplets and may reversibly encyst producing walled, spherical cysts. See Spiegel & al (2006).

It is a rare and recently described species, and it was found only two times during our study.

Specimens examined

Loc. 11: aerial litter of Tilia sp., AS05-104. **Loc. 22:** aerial litter of $Q.\ ilex$, AV07-03.

17. "Protostelium" pyriforme L.S. Olive & Stoian., Amer. J. Bot. 56(9): 987. 1969 [as *pyriformis*]. Figs. 2h, 3p

Sporocarps. Stalk relatively long, 50-100 μ m, narrow, gently tapered, straight to gently curved, with a knob-like apophysis. Spores typically obpyriform or campanulate, 7.5-11.6 \times 8.8. 12.4 μ m, with a small round hilum at the base, often waving in air currents. Prespore cells round to oval (Olive & Stoianovitch, 1969).

Trophic stages. It is mantained in the laboratory on bacteria such as *Escherichia coli*, *Flavobacterium* sp., or *Dyadobacter* sp. strain Malaya, but it does not survive on yeasts. Protoplasts hyaline, mostly uninucleate and with one contractile vacuole. The amoebae in water produce filose pseudopodia. Cysts typically have a scalloped margin, $8.8-15.2 \times 10-17.5 \, \mu m$ (Olive & Stoianovitch, 1969).

It is usually a common species, more abundant in the tropics than in temperate regions (Spiegel & al., 2007), but it was not very common in this study. In Europe, this species has been previously reported from Germany (Tesmer & al., 2005), and Russia (Kosheleva & al., 2009). This species is probably excluded from the genus *Protostelium* and has to be assigned a new genus (see Table 1).

Specimens examined

Loc. 3: aerial litter of *Quercus ilex*, AS05-37. Loc. 5: aerial litter of *Corylus avellana*, AS05-62; ground litter of *Corylus avellana*, AS05-63. Loc. 11: aerial litter of *Rubus* sp., AS05-96. Loc. 14: aerial litter of *R. sphaerocarpa*, M06-43. Loc. 16: aerial litter of *Q. coccifera*, GU06-07. Loc. 17: aerial litter of *R. officinalis*, GU06-13; ground litter of *Q. coccifera*, GU06-16. Loc. 18: aerial litter of thistle, CU06-03. Loc. 19: aerial litter of Gramineae, CU06-05; aerial litter of *Thymus* sp., CU06-07. Loc. 21: aerial litter of *Lavandula* sp., M07-17. Loc. 22: aerial litter of *Q. ilex*, AV07-03. Loc. 24: aerial litter of *Q. pyrenaica*,

AV07-13. Loc. 25: aerial litter of thistle, TO07-13. Loc. 29: aerial litter of Lamiaceae, TE07-30. Loc. 46: ground litter of *J. communis*, SO07-04. Loc. 49: aerial litter of *Cistus albifolius*, CU07-05. Loc. 51: aerial litter of *R. officinalis*, CU07-25. Loc. 55: aerial litter of *Thymus* sp., TE07-15. Loc. 62: aerial litter of *Epilobium hirsutum* and *Lithrum salicaria*, O06-01. Loc. 89: ground litter, H09-35.

18. Schizoplasmodiopsis amoeboidea L.S. Olive & K.D. Whitney, Mycologia 74(4): 655. 1982. Figs. 2h, 3q

Sporocarps. Sporocarps 18-30 μ m tall. Stalks 6-14.4 μ m, straight, suddenly thinner towards their apex forming a sharp point. Spores nearly spherical, 12-22 μ m in diam., single, proportionally big, globose, uninucleate, and non-deciduous, with a minutely punctate surface (Olive & Whitney, 1982). Prespore cells oval to round in outline.

Trophic stages. It can be cultivated on hay infusion agar, oak bark agar, lactose-yeast agar, or wMY in association with *Xanthamonas* sp., *Dyadobacter* sp. strain Malaya or *Flavobacterium* sp. They produce uninucleate (rarely plurinucleate), thin amoeba. The cysts are typically uninucleate and round, 9-37 μ m in diam., or irregular, 7-49 \times 12-72 μ m. See Olive & Whitney (1982).

It is a common species that can be found in many different types of substrate (Spiegel & al., 2007), and was very frequent in our cultures. It has been cited previously in Europe for Germany (Tesmer & al., 2005) and Russia (Kosheleva & al., 2009).

Specimens examined

Loc. 1: ground litter of Pteridium aquilinum, AS05-6; ground litter of Compositae, AS05-12. Loc. 2: ground litter of Cytisus sp., AS05-21; ground litter of thistle, AS05-23; bark of Crataegus monogyna, AS05-26. Loc. 4: ground litter of Calluna vulgaris, AS05-42; bark of Cytisus sp., AS05-45; aerial litter of Erica sp., AS05-48; ground litter of Lamiaceae, AS05-53. Loc. 5: aerial litter of Corylus avellana, AS05-62. Loc. 6: aerial litter of Fagus sylvatica, AS05-64; bark of Fagus sylvatica, AS05-66. Loc. 9: aerial litter of Cytisus sp., AS05-83; ground litter of Cytisus sp., AS05-84. Loc. 10: aerial litter of Erica arborea, AS05-90; aerial litter of Poaceae, AS05-91; ground litter of Poaceae, AS05-92; ground litter of Tilia sp., AS05-94; bark of Pinus sylvestris, AS05-95. Loc. 11: aerial litter of Rubus sp., AS05-96; aerial litter of Tilia sp., AS05-104. Loc. 12: ground litter of Alnus sp., AS05-114. Loc. 13: aerial litter of Lavandula sp., M06-31; ground litter of Lavandula sp., M06-32; aerial litter of Thymus sp., M06-33; ground litter of Thymus sp., M06-34; aerial litter of Q. ilex, M06-35; ground litter of G. scorpius, M06-38. Loc. 15: aerial litter of Gramineae, GU06-01; ground litter of Gramineae, GU06-02; aerial litter of Leguminosae, GU06-03; aerial litter of Lavandula sp., GU06-05; ground litter of Lavandula sp., GU06-06. Loc. 16: aerial litter of Q. coccifera, GU06-07; ground litter of Leguminosae, GU06-10. Loc. 17: aerial litter of Gramineae, GU06-11; ground litter of Gramineae, GU06-12; aerial litter of R. officinalis, GU06-13; ground litter of R. officinalis, GU06-14; aerial litter of Q. coccifera, GU06-15; ground litter of Q. coccifera, GU06-16. Loc. 18: aerial litter of Gramineae, CU06-01; ground litter of Gramineae, CU06-02; ground litter of thistle, CU06-04. Loc. 19: aerial litter of Gramineae, CU06-05; ground litter of Gramineae, CU06-06; aerial litter of Thymus sp., CU06-07; ground litter of Thymus sp., CU06-08. Loc. 20: aerial litter of Lavandula sp., M07-01; ground litter of Lavandula sp., M07-02; aerial litter of Q. ilex, M07-05; bark of Pinus pinea, M07-10. Loc. 21: aerial litter of Q. ilex, M07-11; ground litter of Q. ilex, M07-12; aerial litter of C. salvifolius, M07-13; ground litter of C. salvifolius, M07-14; ground litter of Lavandula sp., M07-18. Loc. 22: aerial litter of Leguminosae, AV07-01; aerial litter of Q. ilex, AV07-03; ground litter of Q. ilex, AV07-04. Loc. 23: aerial litter of Q. ilex, TO07-01; aerial litter of R. sphaerocarpa, TO07-03; ground litter of R. sphaerocarpa, TO07-04; aerial litter of J. oxycedrus, TO07-05; ground litter of J. oxycedrus, TO07-06; aerial litter of Lavandula sp., TO07-07; ground litter of Lavandula sp., TO07-08. Loc. 24: ground litter of Rubus sp., AV07-16; aerial litter of Q. ilex, AV07-17; bark of Q. pyrenaica, AV07-20. Loc. 25: aerial litter of Q. ilex, TO07-11; ground litter

of thistle, TO07-14; bark of O. ilex, TO07-20. Loc. 26: aerial litter of Leguminosae, GU07-05; bark of I. oxycedrus, GU07-09; bark of O. ilex, GU07-10. Loc. 27: aerial litter of Juniperus thurifera, GU07-13; ground litter of Juniperus thurifera, GU07-14; aerial litter of Lavandula sp., GU07-15; bark of Juniperus sp., GU07-16. Loc. 28: aerial litter of Lamiaceae, TE07-19; bark of Q. faginea, TE07-27. Loc. 31: aerial litter of Cistaceae, TE07-47; ground litter of Cistaceae, TE07-48. Loc. 32: aerial litter of R. officinalis, Z07-01; ground litter of R. officinalis, Z07-02; aerial litter of Compositae, Z07-03; aerial litter of Gramineae, Z07-05; bark of I. phoenicea, Z07-09; bark of R. officinalis, Z07-10. Loc. 33: aerial litter of Gramineae, Z07-13; ground litter of Gramineae, Z07-14; bark of Pinus halepensis, Z07-16. Loc. 34: ground litter of Gramineae, Z07-26; aerial litter of P. halepensis, Z07-27. Loc. 35: aerial litter of Lygeum spartum, Z07-31; aerial litter of Arthrocnemum sp., Z07-33; ground litter of Arthrocnemum sp., Z07-34; aerial litter of Suaeda, Z07-35; aerial litter of Suaeda sp., Z07-36; ground litter of Salsola sp., Z07-38. Loc. 36: aerial litter of Lygeum spartum, HU07-01; ground litter of Lygeum spartum, HU07-02; ground litter of Compositae, HU07-06; bark of R. officinalis, HU07-09; bark of *I. phoenicea*, HU07-10. Loc. 37: ground litter of *Ulex* sp., HU07-14; bark of Q. faginea, HU07-19. Loc. 38: bark of Salix sp., HU07-23. Loc. 41: aerial litter of fern, HU07-53. Loc. 42: aerial litter of Rosa sp., NA07-01. Loc. 43: aerial litter of O. coccifera, NA07-16. Loc. 44: aerial litter of Gramineae, NA07-21. Loc. 45: aerial litter of Leguminosae, NA07-23; ground litter of Leguminosae, NA07-24; aerial litter of Atriplex halimus, NA07-33. Loc. 46: ground litter of J. communis, SO07-04. Loc. 47: ground litter of Lamiaceae, SO07-10. Loc. 48: ground litter of Lamiaceae, SO07-18; ground litter of Santolina sp., SO07-20. Loc. 49: aerial litter of O. ilex, CU07-03; ground litter of O. ilex, CU07-04; aerial litter of Cistus albifolius, CU07-05; ground litter of Cistus albifolius, CU07-06; aerial litter of Gramineae, CU07-07; bark of Q. ilex, CU07-09; bark of J. oxycedrus, CU07-10. Loc. 50: ground litter of Compositae, CU07-14; aerial litter of Q. ilex, CU07-15; ground litter of Q. ilex, CU07-16; bark of Pinus sp., CU07-20. Loc. 51: ground litter of Leguminosae, CU07-22; aerial litter of Thymus sp., CU07-23; aerial litter of R. officinalis, CU07-25; ground litter of R. officinalis, CU07-26; aerial litter of Gramineae, CU07-27; ground litter of Gramineae, CU07-28; bark of Pinus nigra, CU07-29. Loc. 52: aerial litter of R. officinalis, CU07-33; ground litter of R. officinalis, CU07-34; ground litter of Q. ilex, CU07-36; aerial litter of Q. ilex, CU07-37; ground litter of Leguminosae, CU07-38. Loc. 53: ground litter of Thymus sp., CU07-42; ground litter of Lavandula sp., CU07-44; aerial litter of Leguminosae, CU07-45; bark of Crataegus monogyna, CU07-50. Loc. 54: aerial litter of Cistus sp., TE07-03; aerial litter of Rosaceae, TE07-06. Loc. 55: aerial litter of Q. ilex, TE07-09; bark of O. ilex, TE07-17. Loc. 56: aerial litter of Retama sphaerocarpa, M06-01; ground litter of Retama sphaerocarpa, M06-02. Loc. 57: aerial litter of Leguminosae, M06-05; ground litter of Leguminosae, M06-06; aerial litter of Gramineae, M06-07; ground litter of Gramineae, M06-08; aerial litter of Leguminosae, M06-09; ground litter of Leguminosae, M06-10; aerial litter of Leguminosae, M06-11; ground litter of Leguminosae, M06-12. Loc. 58: aerial litter of Leguminosae, M06-13; ground litter of Leguminosae, M06-14; aerial litter of Leguminosae, M06-15; ground litter of Leguminosae, M06-16. Loc. 59: aerial litter of Leguminosae, M06-17; ground litter of Leguminosae, M06-18. Loc. 60: ground litter of Leguminosae, M06-22. Loc. 61: aerial litter of Leguminosae, M06-25; ground litter of Leguminosae, M06-26. Loc. 62: aerial litter of Epilobium hirsutum and Lithrum salicaria, O06-01; ground litter of Epilobium hirsutum and Lithrum salicaria, O06-02. Loc. 66: aerial litter of Leguminosae, LE06-03. Loc. 67: ground litter of Leguminosae, PA06-02. Loc. 68: aerial litter, AL07-01. Loc. 71: ground litter, SO06-03. Loc. 77: aerial litter of Lavandula sp., CA09-27. Loc. 87: bark of Q. ilex, H09-29. Loc. 90: aerial litter of Quercus ilex, SE09-01.

19. *Schizoplasmodiopsis micropunctata L.S. Olive & Stoian., Mycologia 67(6): 1097. 1975. Figs. 2i, 3r

Sporocarps. Stalk very variable in length, 9-70 μ m, straight, that gets thinner suddenly at the apex forming a hair-like structure at the point of attachment with the spore. The tip of the stalk may be so thin that the spore almost appears as if it is suspended in the air. Spore globose, 11.3-20.6 μ m in diam., minutely punctuate (Olive & Stoianovitch, 1975). Prespore cells round in outline, formed from single amoebae or segments of the plasmodia.

Trophic stages. It can be cultivated on oak bark agar made with three times the usual amount of oak bark, on supplemented cornmeal agar with half the usual amounts of dextrose and yeast extract, or on wMY agar, grown with bacteria isolated from the original substrate, *Escherichia coli, Flavobacterium* sp., or *Serratia liquefaciens* strain Florida 20 and *Dyadobacter* sp. strain Malaya bacteria as food organisms. The amoebae are thin, uninucleate (sometimes binucleate) and they produce many filose subspeudopodia. They can fuse to produce large, sometimes reticulate plasmodia, but with no nuclear fusion observed. The cysts are round to irregular or reticular, 10-175 × 10-475 µm. See Olive & Stoianovitch (1975).

It is very rare but has been encountered worldwide (Spiegel & al., 2007), and it was identified in only one of our cultures. In Europe, it has been recovered from cultures from Russia (Kosheleva & al., 2009). Spiegel et al. (1995) suggested that this may possibly be a morphotype of *Tychosporium acutostipes*.

Specimens examined

Loc. 12: ground litter of Lamiaceae, AS05-112.

20. Schizoplasmodiopsis pseudoendospora L.S. Olive, M. Martin. & Stoian., in Olive, Mycologia 59(1): 19. 1967.

Figs. 2i, 3s

Sporocarps. Stalks proportionally very short, that taper evenly to their tip. Spores nearly spherical, 6.2-11.5(13) µm in diam. (Olive, 1967). Prespore cells are round to irregular in outline.

Trophic stages. They can be cultivated on hay infusion agar or wMY agar with a mixture of *Flavobacterium* sp. and *Escherichia coli*, or *Serratia liquefaciens* strain Florida 20. Spore germination liberates a single, uninucleate, elongate amoeba, with long and filose pseudopodia. The amoebae can form plasmodia by nuclear division with no plasmotomy, or by fusion of small amoebae. Plasmodia are often branched and anastomosing and may be several millimeters wide. They fragment into uninucleate prespore cells or into cysts. See Olive (1967).

It is one of the smallest but most frequent species, and tends to fruit in big, dense patches. This organism is one of the most common protostelids worldwide, very frequently found in temperate and tropical regions (Spiegel & al., 2007), and it was also very abundant in our samples. In Europe it has been cited from Germany (Tesmer & al., 2005), Ukraine (Glustchenko & al., 2002) and Russia (Kosheleva & al., 2009).

Specimens examined

Loc. 1: aerial litter of *Pteridium aquilinum*, AS05-5; ground litter of *Pteridium aquilinum*, AS05-6; aerial litter of Compositae, AS05-11. Loc. 3: aerial litter of *Cytisus* sp., AS05-31. Loc. 4: ground litter of *Calluna vulgaris*, AS05-42; bark of *Cytisus* sp., AS05-45. Loc. 6: ground litter of *Fagus sylvatica*, AS05-65; bark of *Fagus sylvatica*, AS05-66; aerial litter of *Erica* sp., AS05-68. Loc. 10: ground litter of *Picea abies*, AS05-85; bark of *Picea abies*, AS05-86; ground litter of *Aesculus bippocastanum*, AS05-89; aerial litter of *Erica arborea*, AS05-90; ground litter of *Tilia* sp., AS05-94. Loc. 11: aerial litter of *Rubus* sp., AS05-96; ground litter of *Tilia* sp., AS05-97; aerial litter of *Tilia* sp., AS05-104; ground litter of *Tilia* sp., AS05-105. Loc. 12: aerial litter of *Rubus* sp., AS05-109; bark of *Alnus* sp., AS05-115; ground litter of *Cyperaceae*, AS05-117; ground litter of *Rumex* sp., AS05-118. Loc. 13: ground litter of *Gramineae*, M06-30; aerial litter of *Lavandula* sp., M06-31; aerial litter of *Thymus* sp., M06-31; aerial litter of *Thymus* sp., M06-34; aerial litter of

O. ilex, M06-35; ground litter of O. ilex, M06-36; aerial litter of G. scorpius, M06-37; ground litter of G. scorpius, M06-38. Loc. 14: aerial litter of C. ladanifer, M06-39; ground litter of C. ladanifer, M06-40; aerial litter of Gramineae, M06-41; ground litter of Gramineae, M06-42; ground litter of R. sphaerocarpa, M06-44. Loc. 15: aerial litter of Gramineae, GU06-01; ground litter of Gramineae, GU06-02; ground litter of Leguminosae, GU06-04; aerial litter of Lavandula sp., GU06-05; ground litter of Lavandula sp., GU06-06. Loc. 16: aerial litter of Q. coccifera, GU06-07; ground litter of Q. coccifera, GU06-08. Loc. 17: aerial litter of Gramineae. GU06-11: aerial litter of R. officinalis, GU06-13; ground litter of R. officinalis, GU06-14; aerial litter of Q. coccifera, GU06-15; ground litter of Q. coccifera, GU06-16. Loc. 18: ground litter of Gramineae, CU06-02; ground litter of thistle, CU06-04. Loc. 19: ground litter of Gramineae, CU06-06; aerial aerial litter of Thymus sp., CU06-07. Loc. 20: aerial litter of Lavandula sp., M07-01; aerial litter of Q. ilex, M07-05; ground litter of Q. ilex, M07-06. Loc. 21: ground litter of Q. ilex, M07-12; aerial litter of C. salvifolius, M07-13; ground litter of C. salvifolius, M07-14; aerial litter of Gramineae, M07-15; aerial litter of Lavandula sp., M07-17; ground litter of Lavandula sp., M07-18. Loc. 22: ground litter of Leguminosae, AV07-02; aerial litter of Q. ilex, AV07-03; ground litter of Q. ilex, AV07-04; ground litter of J. oxycedrus, AV07-08; bark of Q. ilex, AV07-09; bark of J. oxycedrus, AV07-10. Loc. 23: aerial litter of Q. ilex, TO07-01; ground litter of Q. ilex, TO07-02; ground litter of R. sphaerocarpa, TO07-04; aerial litter of J. oxycedrus, TO07-05; ground litter of J. oxycedrus, TO07-06; aerial litter of Lavandula sp., TO07-07; ground litter of Lavandula sp., TO07-08. Loc. 24: ground litter of C. ladanifer, AV07-12; aerial litter of Q. pyrenaica, AV07-13; ground litter of Q. pyrenaica, AV07-14; ground litter of Rubus sp., AV07-16; aerial litter of Q. ilex, AV07-17; ground litter of Q. ilex, AV07-18; bark of O. pyrenaica, AV07-20. Loc. 25: ground litter of O. ilex, TO07-12; ground litter of thistle, TO07-14; aerial litter of Lavandula sp., TO07-17; ground litter of Lavandula sp., TO07-18; bark of Q. ilex, TO07-20. Loc. 26: bark of J. oxycedrus, GU07-09; bark of Q. ilex, GU07-10. Loc. 27: aerial litter of Juniperus thurifera, GU07-13; aerial litter of Lavandula sp., GU07-15; bark of Juniperus sp., GU07-16; aerial litter of Leguminosae, GU07-17; bark of Ulmus sp., GU07-20. Loc. 28: ground litter of Lamiaceae, TE07-20; bark of Q. faginea, TE07-27. Loc. 31: aerial litter of Q. coccifera, TE07-43; ground litter of Q. coccifera, TE07-44; ground litter of Lamiaceae, TE07-46; aerial litter of Cistaceae, TE07-47; ground litter of Cistaceae, TE07-48; aerial litter of Gramineae, TE07-49; bark of Olea europaea, TE07-52. Loc. 32: aerial litter of *R. officinalis*, Z07-01; ground litter of *R. officinalis*, Z07-02; aerial litter of Compositae, Z07-03; ground litter of Artemisia sp., Z07-04; ground litter of Gramineae, Z07-06; ground litter of Leguminosae, Z07-08. Loc. 33: ground litter of R. officinalis, Z07-12; ground litter of Gramineae, Z07-14; aerial litter of Ephedra sp., Z07-17; ground litter of Ephedra sp., Z07-18. Loc. 34: aerial litter of R. officinalis, Z07-21; ground litter of R. officinalis, Z07-22; bark of Juniperus sp., Z07-23; aerial litter of P. halepensis, Z07-27. Loc. 35: ground litter of Arthrocnemum sp., Z07-34; aerial litter of Suaeda sp., Z07-36. Loc. 36: ground litter of Compositae, HU07-06; bark of R. officinalis, HU07-09; bark of J. phoenicea, HU07-10. Loc. 37: bark of Q. faginea, HU07-19. Loc. 38: bark of Salix sp., HU07-23; aerial litter of Geum sp., HU07-27. Loc. 39: ground litter of F. sylvatica, HU07-32; ground litter of Quercus sp., HU07-33. Loc. 41: ground litter of fern, HU07-54. Loc. 42: ground litter of Rosa sp., NA07-02; aerial litter of Gramineae, NA07-07; ground litter of Gramineae, NA07-08. Loc. 43: ground litter of Q. humilis, NA07-10; ground litter of Q. coccifera, NA07-14; ground litter of Gramineae, NA07-15. Loc. 44: ground litter of Q. coccifera, NA07-20. Loc. 45: ground litter of Leguminosae, NA07-24; ground litter of Gramineae, NA07-26; ground litter of Cistaceae, NA07-28; ground litter of R. officinalis, NA07-30; aerial litter of Atriplex halimus, NA07-33. Loc. 48: ground litter of Lamiaceae, SO07-18; ground litter of Santolina sp., SO07-20. Loc. 49: aerial litter of R. officinalis, CU07-01; ground litter of Q. ilex, CU07-04; aerial litter of Cistus albifolius, CU07-05; bark of Q. ilex, CU07-09; bark of J. oxycedrus, CU07-10. Loc. 50: aerial litter of Thymus sp., CU07-11; ground litter of Compositae, CU07-14; aerial litter of Q. ilex, CU07-15; ground litter of Q. ilex, CU07- 16; bark of Q. ilex, CU07-19; bark of Pinus sp., CU07-20. Loc. 51: aerial litter of Thymus sp., CU07-23; ground litter of Thymus sp., CU07-24; ground litter of R. officinalis, CU07-26; bark of Pinus nigra, CU07-29; bark of Juniperus sp., CU07-30. Loc. 52: ground litter of Q. coccifera, CU07-32; aerial litter of R. officinalis, CU07-33; ground litter of Q. ilex, CU07-36; ground litter of Leguminosae, CU07-38. Loc. 53: aerial litter of Thymus sp., CU07-41; ground litter of Thymus sp., CU07-42; aerial litter of Leguminosae, CU07-45; bark of Crataegus monogyna, CU07-50. Loc. 54: aerial litter of Cistus sp., TE07-03; aerial litter of Cistus sp., TE07-04. Loc. 55: aerial litter of O. ilex, TE07-09; ground litter of Q. ilex, TE07-10; ground litter of Leguminosae, TE07-14; bark of Q. ilex, TE07-17. Loc. 56: aerial litter of Retama sphaerocarpa, M06-01; ground litter of Retama sphaerocarpa, M06-02. Loc. 57: aerial litter of Leguminosae, M06-05; aerial litter of Leguminosae, M06-09; ground litter of Leguminosae, M06-10; ground litter of Leguminosae, M06- 12. Loc. 58: aerial litter of Leguminosae, M06-13; ground litter of Gramineae, M06-16. Loc. 59: aerial litter of Leguminosae, M06-17; ground litter of Leguminosae, M06-18, Loc. 60; ground litter of Leguminosae, M06-22. Loc. 61: ground litter of Leguminosae, M06-26. Loc. 62: aerial litter of Epilobium hirsutum and Lithrum salicaria, O06-01; ground litter of Epilobium hirsutum and Lithrum salicaria, O06-02. Loc. 64: aerial litter of Leguminosae, LU06-01; ground litter of Leguminosae, LU06-02. Loc. 65: aerial litter of Chamaespartium tridentatum, LU06-03; ground litter of Chamaespartium tridentatum, LU06-04. Loc. 66: aerial litter of Leguminosae, LE06-03. Loc. 67: aerial litter of Leguminosae, PA06-01; ground litter of Leguminosae, PA06-02. Loc. 69: ground litter, SO06-01. Loc. 71: ground litter, SO06-03. Loc. 72: ground litter, SO06-04. Loc. 73: aerial litter of Hacer monspessulanum, GE08-07. Loc. 74: aerial litter of fern, GE08-15; aerial litter of Rosaceae, GE08-17; ground litter of Rosaceae, GE08-18; bark of Fagus sylvatica, GE08-20. Loc. 76: ground litter of Q. ilex, CA09-14. Loc. 77: ground litter of *Q. faginea*, CA09-22. Loc. 78: ground litter of *Q. ilex*, CA09-38. Loc. 81: ground litter of Cistus sp., BA09-22; ground litter of Lamiaceae, BA09-28. Loc. 83: ground litter of Cistus sp., H09-12; ground litter of Gramineae, H09-16. Loc. 85: aerial litter of Lavandula sp., PO09-17. Loc. 90: ground litter of Q. ilex, SE09-02. Loc. 92: ground litter of Q. ilex, CO09-04; aerial litter of Cistus sp., CO09-07. Loc. 93: ground litter, CO09-12. Loc. 95: ground litter, PO09-41. Loc. 96: ground litter of Rosaceae, FR08-08.

21. *Schizoplasmodiopsis reticulata L.S. Olive & Stoian., Mycologia 67(6): 1089. 1975. Fig. 2i

Sporocarps. Sporocarps very variable in length, 45-110 μ m. Gracile stalks, 38-90 μ m long. Spores spherical, 7-20 μ m in diam., with a reticulum of ridges on their surface (Olive & Stoianovitch, 1975). Prespore cells round, formed from single amoebae or segments of plasmodia.

Trophic stages. It can be cultivated on oak-bark agar (Olive, 1975) or wMY agar, in association with bacteria isolated from its original substrate or bacterium Serratia liquefaciens strain Florida 20. The spores produce a single uninucleate amoeba, which is branched with numerous, often branched filose subpseudopodia. They can fuse to produce large plasmodia but no nuclear fusion is observed. The cysts are globose to oblong or irregular, 7-32 × 7-58 µm. See Olive & Stoianovitch (1975).

This is a relatively rare species, but it is widespread. It occurs in situations wherever *S. vulgare* is likely to be found (Spiegel & al., 2007). It was found only once during our study.

Specimens examined

Loc. 31: bark of Olea europaea, TE07-52.

22. Schizoplasmodiopsis vulgaris L.S. Olive & Stoian., Mycologia 67(6): 1092. 1975 [as *vulgare*]. Figs. 2j, 3t

Sporocarps. Stalk relatively thick and very variable in length, 9-70 µm long, tapering to a blunt apex but not tapering to a fine point. Spores, 8-16(37) µm in diam., nearly spherical and coarse, with low ridges formed by a reticulum of spore wall thickenings that appear as slight bumps (Olive & Stoianovitch, 1975). Prespore cells circular in outline, and usually many of them are formed simultaneously due to fragmentation of the plasmodium.

Trophic stages. It can be grown on hay infusion agar, oak bark agar, lactose-yeast agar or wMY agar on association with

pregrown bacterium Florida 20 or *Flavobacterium* sp.. Each spore gives rise to a single, thin, branched amoeba with filose subpseudopodia and several contractilve vacuoles. They can fuse to produce large plasmodia with no nuclear fusion observed. The cysts are round to irregular, uninucleate to plurinucleate, $5-66 \times 7-300 \, \mu m$. See Olive & Stoianovitch (1975).

This species has been cited in Europe for England (Olive 1975b), Germany (Tesmer & al., 2005), and Russia (Kosheleva & al., 2009). It is a common species worldwide, and in cool, moist habitats, it is often one of the few species encountered (Spiegel & al., 2007). It was quite common in our cultures from the Iberian Peninsula.

Specimens examined

Loc. 1: aerial litter of Pteridium aquilinum, AS05-5; ground litter of Pteridium aquilinum, AS05-6; ground litter of Compositae, AS05-12. Loc. 6: ground litter of Fagus sylvatica, AS05-65. Loc. 12: ground litter of Rubus sp., AS05-110; ground litter of Equisetum sp., AS-121. Loc. 13: aerial litter of Lavandula sp., M06-31; ground litter of Lavandula sp., M06-32; aerial litter of Q. ilex, M06-35; ground litter of G. scorpius, M06-38. Loc. 14: aerial litter of Gramineae, M06-41; aerial litter of R. sphaerocarpa, M06-43. Loc. 15: aerial litter of Leguminosae, GU06- 03. Loc. 17: ground litter of Gramineae, GU06-12; aerial litter of R. officinalis, GU06-13; aerial litter of Q. coccifera, GU06-15. Loc. 19: aerial litter of Gramineae, CU06-05; ground litter of Thymus sp., CU06-08. Loc. 20: aerial litter of Lavandula sp., M07-01; aerial litter of R. sphaerocarpa, M07-03; ground litter of R. sphaerocarpa, M07-04. Loc. 21: aerial litter of *Q. ilex*, M07-11. Loc. 22: ground litter of *Q. ilex*, AV07-04. Loc. 23: ground litter of R. sphaerocarpa, TO07-04; aerial litter of Lavandula sp., TO07-07. Loc. 24: aerial litter of Q. pyrenaica, AV07-13. Loc. 25: aerial litter of Q. ilex, TO07-11; bark of Q. ilex, TO07-20. Loc. 27: aerial litter of Juniperus thurifera, GU07-13. Loc. 31: bark of Olea europaea, TE07-52. Loc. 32: aerial litter of R. officinalis, Z07-01. Loc. 36: ground litter of Compositae, HU07-06. Loc. 45: aerial litter of Atriplex halimus, NA07-33. Loc. 47: ground litter of Lamiaceae, SO07-10. Loc. 49: aerial litter of R. officinalis, CU07-01; aerial litter of Cistus albifolius, CU07-05; ground litter of Gramineae, CU07-08. Loc. 50: ground litter of Q. ilex, CU07-16. Loc. 51: ground litter of R. officinalis, CU07-26; bark of Juniperus sp., CU07-30. Loc. **56:** aerial litter of *Retama sphaerocarpa*, M06-01: ground litter of *Retama* sphaerocarpa, M06-02. Loc. 57: ground litter of Leguminosae, M06-06; aerial litter of Leguminosae, M06-11. Loc. 58: ground litter of Leguminosae, M06-14; ground litter of Gramineae, M06-16. Loc. 59: ground litter of Leguminosae, M06-18. Loc. 60: ground litter of Leguminosae, M06-22. Loc. 61: ground litter of Leguminosae, M06-26. Loc. 62: ground litter of Epilobium hirsutum and Lithrum salicaria, O06-02. Loc. 66: aerial litter of Leguminosae, LE06-03. Loc. 74: bark of Quercus sp., GE08-19. Loc. 87: aerial litter of compositae, H09-27.

23. Schizoplasmodium cavostelioides L.S. Olive & Stoian., Amer. J. Bot 53(4): 344. 1966. Figs. 2l, 3u

Sporocarps. Sporocarps ballistosporous. Stalk relatively short, 4.3-8 μ m, thick, with a distinct goblet-shaped apophysis. Spore almost spherical, relatively big, 11-20.5 μ m in diam., smooth, typically multinucleated, attached to the stalk by a ring-shaped hilum that fits the apophysis (Olive & Stoianovitch, 1966b). Just before the spore discharge, a swelling of the sheath, interpreted as a gas bubble or a liquid droplet, appears. Prespore cells are round from above and hat-shaped from the side.

Trophic stages. It grows well on hay infusion agar with Kitani, or mixture of Kitani and *Dyadobacter* sp. strain Malaya bacterium. It forms plasmodia that can be reticulate, eventually fragmenting into few to many multinucleate prespore cells. The cysts are very variable in size and shape, 12-30 × 13.5-50 µm. See Olive & Stoianovitch (1966b).

It is a fairly common species in temperate areas and also common in the tropics (Spiegel & al., 2007), and was not uncommon in present study. This species has been reported previously only from Germany (Tesmer & al., 2005) in Europe.

Specimens examined

Loc. 1: ground litter of Pteridium aquilinum, AS05-6; aerial litter of Compositae, AS05-11. Loc. 6: bark of Fagus sylvatica, AS05-66; aerial litter of Erica sp., AS05-68. Loc. 12: aerial litter of Rubus sp., AS05-109. Loc. 20: ground litter of R. sphaerocarpa, M07-04. Loc. 21: aerial litter of Gramineae, M07-15. Loc. 27: bark of Juniperus sp., GU07-16; ground litter of Leguminosae, GU07-18. Loc. 29: ground litter of Gramineae, TE07-33. Loc. 32: ground litter of R. officinalis, Z07-02; bark of J. phoenicea, Z07-09. Loc. 33: bark of R. officinalis, Z07-15; bark of Pinus halepensis, Z07-16, Loc. 35; aerial litter of Arthrocnemum sp., Z07-33. Loc. 36: aerial litter of Lygeum spartum, HU07-01; bark of R. officinalis, HU07-09; bark of J. phoenicea, HU07-10. Loc. 44: ground litter of O. coccifera, NA07-20. Loc. 45: ground litter of Leguminosae, NA07-24; aerial litter of Cistaceae, NA07-27. Loc. 47: ground litter of Leguminosae, SO07-16. Loc. 49: bark of J. oxycedrus, CU07-10. Loc. 51: ground litter of Leguminosae, CU07-22; ground litter of Gramineae, CU07-28; bark of Pinus nigra, CU07-29; bark of Juniperus sp., CU07-30. Loc. **52:** aerial litter of *Q. ilex*, CU07-37. **Loc. 54:** aerial litter of *Cistus* sp., TE07-03. Loc. 62: ground litter of Epilobium hirsutum and Lithrum salicaria, O06-02. Loc. 74: aerial litter of Fagus sylvatica, GE08-11; aerial litter of Castanea sativa, GE08-13.

24. *Soliformovum expulsum (L.S. Olive & Stoian.) Spiegel, in Spiegel, Gecks & Feldman, J. Eukaryotic Microbiol. 41(5): 518. 1994. ≡ *Protostelium expulsum* L.S. Olive & Stoian., Trans. Brit. Mycol. Soc. 76(2): 303. 1981.

Fig. 2k

Sporocarps. Sporocarps 32.5-45 μm tall, ballistosporous. Stalk bipartite with a broadly tapered basal section and a uniformly thin apical section, usually sharply reflexed at the junction of the two sections. Spores spherical, single, 11.3-17.4 μm diam., forcibly discharged with the disappearance of the stalk (Olive & Stoianovitch, 1981). Prespore cells "fried-egg" shaped.

Trophic stages. It can be cultivated on oak bark agar (at pH 7) or wMY with *Xanthomonas* sp. and *Dyadobacter* sp. strain Malaya as food organisms. It produces amoeboid and non-flagellate cells, usually flabellate during migration. They are typically uninucleate, and occasionally binucleate. Their nucleolus is irregular and often multilobed. The cysts are round, 9-33.6 μ m diam., oval, or irregular in shape, 7.2-22.8 \times 9.6-26.4 μ m, uninucleate. The nucleolus of the cyst nucleus generally has a more regular shape than those of amoeboid cells. See Spiegel & al. (1994).

It was originally described as *Protostelium expulsum* L.S. Olive & Stoian. It is not uncommon and somewhat more abundant in the tropics than in temperate habitats (Spiegel & al., 2007), but it has been found only once during our study.

Specimens examined

Loc. 6: bark of *Fagus sylvatica*, AS05-66. **Loc. 11:** aerial litter of *Rubus* sp., AS05-96. **Loc. 61:** ground litter of *Leguminosae*, M06-26.

25. Soliformovum irregulare (L.S. Olive & Stoian.) Spiegel, in Spiegel, Gecks & Feldman, J. Eukaryotic Microbiol. 41(5): 518. 1994 [as *irregularis*]. ≡ *Protostelium irregulare* L.S. Olive & Stoian., Amer. J. Bot. 56(9): 983. 1969.

Figs. 2k, 3v

Sporocarps. Spores nearly spherical, 13.9-22.5 μ m in diam. Stalks proportionally long, 30-127 μ m, straight, gently tapered with a hastate apophysis (Olive & Stoianovitch, 1969). Spore deciduous, that can adhere to the side of the stalk after falling, and becomes "American football"-shaped when dryed. Prespore cells are "fried-egg" shaped.

Trophic stages. It feeds on Flavobacterium sp. or Escherichia coli. Amoebae typically uninucleate (but also plurinucleate). The nucleolus is divided into many small, phase dense subunits, and the nucleus may be irregular in outline. The amoebae are very thin, almost invisible on the agar surface when viewed with bright field optics, and slightly bigger than those of *S. expulsum*. The amoebae have numerous, small contractile vacuoles and many food vacuoles when they are feeding. They are typically flabellate when migrating, with a broad lamellopodial front. There are numerous acutely pointed subseudopodia which can become quite elongated under very moist conditions. Motility appears to be solely by pseudopodial crawling and gliding has not been observed. See Spiegel & al. (1994).

It is one of the most common species in temperate areas and worldwide (Spiegel & al., 2007), and it was also quite common in our cultures. In Europe, this species have been cited from Germany (Tesmer & al., 2005) and Russia (Kosheleva & al., 2009).

Specimens examined

Loc. 1: aerial litter of Compositae, AS05-11. Loc. 2: aerial litter of Cytisus sp., AS05-20; bark of Crataegus monogyna, AS05-26. Loc. 3: aerial litter of Cytisus sp., AS05-31; aerial litter of Lamiaceae, AS05-39. Loc 4: aerial litter of Mentha sp., AS05-52. Loc. 5: ground litter of Corylus avellana, AS05-63. Loc. 6: aerial litter of Erica sp., AS05-68. Loc. 8: aerial litter of Poaceae, AS05-77. Loc. 11: aerial litter of Rubus sp., AS05-96; aerial litter of Compositae, AS05-102; aerial litter of Tilia sp., AS05-104. Loc. 12: ground litter of Lamiaceae, AS05-112; ground litter of Alnus sp., AS05-114; ground litter of Cyperaceae, AS05-117; ground litter of Rumex sp., AS05-118; ground litter of Equisetum sp., AS-121. Loc. 13: aerial litter of Thymus sp., M06-33; aerial litter of Q. ilex, M06-35. Loc. 14: aerial litter of C. ladanifer, M06-39; ground litter of Gramineae, M06-42. Loc. 16: aerial litter of Q. coccifera, GU06-07. Loc. 17: aerial litter of Gramineae, GU06-11; ground litter of Gramineae, GU06-12; aerial litter of R. officinalis, GU06-13; aerial litter of Q. coccifera, GU06-15. Loc. 19: aerial aerial litter of Thymus sp., CU06-07; ground litter of Thymus sp., CU06-08. Loc. 24: aerial litter of Q. pyrenaica, AV07-13. Loc. 25: aerial litter of Lavandula sp., TO07-17. Loc. 26: ground litter of Q. coccifera, GU07-08. Loc. 27: bark of *Ulmus* sp., GU07-20. Loc. 28: aerial litter of Lamiaceae, TE07-19; ground litter of Lamiaceae, TE07-20. Loc. 29: ground litter of Lamiaceae, TE07-31. Loc. 31: ground litter of Cistaceae, TE07-48; aerial litter of Gramineae, TE07-49; bark of Olea europaea, TE07-52. Loc. 32: aerial litter of R. officinalis, Z07-01; ground litter of R. officinalis, Z07-02; aerial litter of Compositae, Z07-03. Loc. 33: ground litter of Gramineae, Z07-14. Loc. 35: ground litter of Lygeum spartum, Z07-32; ground litter of Arthrocnemum sp., Z07-34; aerial litter of Suaeda sp., Z07-36. Loc. 36: ground litter of Compositae, HU07-06. Loc. 41: aerial litter of fern, HU07-53. Loc. 43: aerial litter of Q. coccifera, NA07-16. Loc. 47: ground litter of Lamiaceae, SO07-10. Loc. 48: ground litter of Lamiaceae, SO07-18; aerial litter of Santolina sp., SO07-19; ground litter of Santolina sp., SO07-20; aerial litter of Gramineae, SO07-22. Loc. 49: aerial litter of R. officinalis, CU07-01; ground litter of Cistus albifolius, CU07-06. Loc. 50: aerial litter of Compositae, CU07-13. Loc. 51: ground litter of *Thymus* sp., CU07-24; aerial litter of *R. officinalis*, CU07-25; ground litter of R. officinalis, CU07-26; bark of Pinus nigra, CU07-29. Loc. 52: aerial litter of R. officinalis, CU07-33. Loc. 57: aerial litter of Leguminosae, M06-05; aerial litter of Gramineae, M06-07. Loc. 62: aerial litter of Epilobium hirsutum and Lithrum salicaria, O06-01. Loc. 67: ground litter of Leguminosae, PA06-02. Loc. 73: aerial litter of Acer monspessulanum, GE08-07. Loc. 74: ground litter of Castanea sativa, GE08-14; ground litter of fern, GE08-16. Loc. 82: aerial litter of Lamiaceae, H09-07.

26. Tychosporium acutostipes Spiegel, D.L. Moore & J. Feldman, Mycologia 87(2): 265. 1995. Figs. 2l, 3w

Sporocarps. Stalks (6.9)35-64 µm long, with a somewhat undulate surface, stiff, gradually thinner towards their apex, sharp-poited, undulated. Spores turbinate to nearly spherical, 8.0-12.5 µm in diam., uninucleate, relatively indeciduous (Spiegel & al., 1995), sometimes "American football"-shaped when dryed. In air currents spores can incline to one side, but remaining attached to the stalk. Prespore cells are ellipsoidal.

Trophic stages. It grows and fruits well on wMY agar with either Fla-20 or *Flavobacterium* sp. as its food source. The amoebae are typically uninucleate and unpigmented, though they may become plurinucleate in older cultures. See Spiegel & al. (1995).

Though it is usually a relatively uncommon species, it is found worldwide (Spiegel & al., 2007) and was abundant in our cultures. In Europe, this species has been cited for Germany (Tesmer & al., 2005) and Russia (Kosheleva & al., 2009).

Specimens examined

Loc. 1: ground litter of Pteridium aquilinum, AS05-6. Loc. 2: ground litter of Cytisus sp., AS05-21. Loc. 3: aerial litter of Lamiaceae, AS05-39. Loc. 4: ground litter of Lamiaceae, AS05-53. Loc. 6: ground litter of fern, AS05-67; aerial litter of Erica sp., AS05-68. Loc. 9: ground litter of Gentiana lutea, AS05-80. Loc. 10: ground litter of Picea abies, AS05-85. Loc. 11: aerial litter of Rubus sp., AS05-96; ground litter of Campanula sp., AS05-101; ground litter of Compositae, AS05-103. Loc. 12: aerial litter of Lamiaceae, AS05-111; ground litter of Lamiaceae, AS05-112; ground litter of Rumex sp., AS05-118. Loc. 13: ground litter of Gramineae, M06-30; aerial litter of Lavandula sp., M06-31; ground litter of Lavandula sp., M06-32; aerial litter of Thymus sp., M06-33; ground litter of *Thymus* sp., M06-34; aerial litter of *Q. ilex*, M06-35; ground litter of G. scorpius, M06-38. Loc. 14: ground litter of Gramineae, M06-42; aerial litter of R. sphaerocarpa, M06-43. Loc. 15: ground litter of Gramineae, GU06-02; aerial litter of Leguminosae, GU06-03; ground litter of Leguminosae, GU06-04; aerial litter of Lavandula sp., GU06-05; ground litter of Lavandula sp., GU06-06. Loc. 16: aerial litter of Q. coccifera, GU06-07; ground litter of Q. coccifera, GU06-08. Loc. 17: aerial litter of Gramineae, GU06-11; ground litter of Gramineae, GU06-12; aerial litter of R. officinalis, GU06-13; ground litter of R. officinalis, GU06-14; aerial litter of Q. coccifera, GU06-15. Loc. 18: ground litter of Gramineae, CU06-02; ground litter of thistle, CU06-04. Loc. 19: aerial litter of Gramineae, CU06-05; ground litter of Gramineae, CU06-06; aerial litter of Thymus sp., CU06-07; ground litter of Thymus sp., CU06-08. Loc. 20: aerial litter of Lavandula sp., M07-01; ground litter of Lavandula sp., M07-02. Loc. 21: ground litter of C. salvifolius, M07-14; aerial litter of Lavandula sp., M07-17; ground litter of Lavandula sp., M07-18. Loc. 22: aerial litter of Leguminosae, AV07-01; bark of Q. ilex, AV07-09. Loc. 23: aerial litter of Q. ilex, TO07-01; aerial litter of R. sphaerocarpa, TO07-03; ground litter of R. sphaerocarpa, TO07-04; ground litter of J. oxycedrus, TO07-06. Loc. 24: aerial litter of C. ladanifer, AV07-11; aerial litter of Q. pyrenaica, AV07-13; ground litter of Rubus sp., AV07-16. Loc. 25: aerial litter of thistle, TO07-13; ground litter of thistle, TO07-14; ground litter of C. ladanifer, TO07-16; aerial litter of Lavandula sp., TO07-17; ground litter of Lavandula sp., TO07-18. Loc. 26: aerial litter of Santolina sp., GU07-03; aerial litter of Thymus sp., GU07-07; ground litter of Q. coccifera, GU07-08. Loc. 27: ground litter of Gramineae, GU07-12; ground litter of Leguminosae, GU07-18; bark of Ulmus sp., GU07-20. Loc. 28: aerial litter of Lamiaceae, TE07-19; ground litter of Lamiaceae, TE07-20; ground litter of Q. faginea, TE07-26. Loc. 29: ground litter of Lamiaceae, TE07-31. Loc. 31: ground litter of O. coccifera, TE07-44; aerial litter of Lamiaceae, TE07-45; aerial litter of Cistaceae, TE07-47; aerial litter of Gramineae, TE07-49. Loc. 32: aerial litter of Compositae, Z07-03; ground litter of Artemisia sp., Z07-04. Loc. 33: ground litter of Gramineae, Z07-14. Loc. 34: ground litter of Gramineae, Z07-26. Loc. 35: aerial litter of Lygeum spartum, Z07-31. Loc. 36: aerial litter of Lygeum spartum, HU07-01; ground litter of Lygeum spartum, HU07-02; aerial litter of Lamiaceae, HU07-03; ground litter of Compositae, HU07-06; bark of J. phoenicea, HU07-10. Loc. 37: ground litter of Buxus sempervirens, HU07-12; bark of J. communis, HU07-20. Loc. 41: aerial litter of fern, HU07-53; ground litter of fern, HU07-54. Loc. 42: aerial litter of Rosa sp., NA07-01; aerial litter of Gramineae, NA07-07. Loc. 43: ground litter of Leguminosae, NA07-12; aerial litter of Gramineae, NA07-13. Loc. 44: ground litter of Q. coccifera, NA07-20. Loc. 45: aerial litter of Leguminosae, NA07-23; ground litter of Leguminosae, NA07-24; aerial litter of Gramineae, NA07-25; ground litter of Gramineae, NA07-26; ground litter of Cistaceae, NA07-28; ground litter of R. officinalis, NA07-30; ground litter of Compositae, NA07-32; aerial litter of Atriplex halimus, NA07-33. Loc. 47: aerial litter of Lamiaceae, SO07-09. Loc. 48: ground litter of Lamiaceae, SO07-18; ground litter of Santolina sp., SO07-20. Loc. 49: aerial litter of R. officinalis, CU07-01; ground litter of R. officinalis, CU07-02; ground litter of Q. ilex, CU07-04; aerial litter of Cistus albifolius, CU07-05; aerial litter of Gramineae, CU07-07; ground litter of Gramineae, CU07-08; bark of *J. oxycedrus*, CU07-10. Loc. 50: aerial litter of *Thymus* sp., CU07-11; ground litter of Thymus sp., CU07-12. Loc. 51: aerial litter of Leguminosae, CU07-21; ground litter of Leguminosae, CU07-22; aerial litter of *Thymus* sp., CU07-23; ground litter of Thymus sp., CU07-24; aerial litter of R. officinalis, CU07-25. Loc. 52: aerial litter of Q. ilex, CU07-35; ground litter of Q. ilex, CU07-36. Loc. 53: ground litter of Thymus sp., CU07-42; ground litter of Leguminosae, CU07-46. Loc. 54: aerial litter of Cistus sp., TE07-03. Loc. 55: aerial litter of Q. ilex, TE07-09; ground litter of Q. ilex, TE07-10; ground litter of Leguminosae, TE07-14; aerial litter of Thymus sp., TE07-15; ground litter of Thymus sp., TE07-16. Loc. 56: aerial litter of Retama sphaerocarpa, M06-01; ground litter of *Retama sphaerocarpa*, M06-02. Loc. 57: aerial litter of Leguminosae, M06-09; ground litter of Leguminosae, M06-10; ground litter of Leguminosae, M06-12. Loc. 58: ground litter of Leguminosae, M06-14. Loc. 60: ground litter of Leguminosae, M06-22. Loc. 62: aerial litter of Epilobium hirsutum and Lithrum salicaria, O06-01; ground litter of Epilobium hirsutum and Lithrum salicaria, O06-02. Loc. 63: aerial litter of Gramineae, LE06-01; ground litter of Gramineae, LE06-02. Loc. 64: ground litter of Leguminosae, LU06-02. Loc. 72: ground litter, SO06-04. Loc. 74: aerial litter of fern, GE08-15; ground litter of fern, GE08-16. Loc. 84: ground litter of Q. ilex, PO09-04. Loc. 86: ground litter of Cistus sp., PO09-22; ground litter of Q. suber, PO09-28. Loc. 92: ground litter of Cistus sp., CO09-08.

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APPENDIX 1

Sampled localities and their characteristics.

	Locality	Coordinates		Elevation	Sampling date	Voucher numbers
Loc. 1	SPAIN. Asturias: Teverga, Vigidel, road TE-1	43.14636°N	6.14100°W	630 m	4-X-2005	AS05-1 – AS05-12
Loc. 2	SPAIN. Asturias: Teverga, Puerto de San Lorenzo, road TE-1	43.14056°N	6.19333°W	1310 m	4-X-2005	AS05-13 - AS05-26
Loc. 3	SPAIN. Asturias: Somiedo, Las Viñas	43.15278°N	6.26472°W	740 m	4-X-2005	AS05-27 - AS05-40
Loc. 4	SPAIN. Asturias: Somiedo, Puerto de Somiedo, road CV-77-3	42.99541°N	6.20290°W	1427 m	4-X-2005	AS05-41 - AS05-53
Loc. 5	SPAIN. Asturias: Somiedo, Saliencia, Endriga	43.10909°N	6.15511°W	1300 m	5-X-2005	AS05-54 - AS05-63
Loc. 6	SPAIN. Asturias: Somiedo, Saliencia, Endriga	43.09000°N	6.15475°W	1120 m	5-X-2005	AS05-64 - AS05-69
Loc. 7	SPAIN. Asturias: Somiedo, Braña Campa d'Abaxu	43.07860°N	6.13067°W	1202 m	5-X-2005	AS05-70 - AS05-71
Loc. 8	SPAIN. Asturias: Somiedo, Saliencia lakes	43.05541°N	6.09935°W	1610 m	5-X-2005	AS05-72 - AS05-78
Loc. 9	SPAIN. Asturias: Somiedo, Alto de la Farragona	43.06147°N	6.09975°W	1549 m	5-X-2005	AS05-79 - AS05-84
Loc. 10	SPAIN. Asturias: Somiedo, La Malva electric power station	43.11275°N	6.24660°W	700 m	5-X-2005	AS05-85 - AS05-95
Loc. 11	SPAIN. Asturias: Somiedo, La Venta Castru, road to Pineda	43.12916°N	6.26738°W	534 m	6-X-2005	AS05-96 - AS05-108
Loc. 12	SPAIN. Asturias: Somiedo, Río Pigüeña	43.14482°N	6.33294°W	569 m	6-X-2005	AS05-109 - AS05-121
Loc. 13	SPAIN. Madrid: Torrelaguna, road N-320, km 337	40.81250°N	3.58778°W	815 m	26-X-2006	M06-29 - M06-38
Loc. 14	SPAIN. Madrid: Casa de Uceda, Pontón de la Oliva	40.88583°N	3.45528°W	868 m	26-X-2006	M06-39 - M06-44
Loc. 15	SPAIN. Guadalajara: Uceda, road to Cubillos de Uceda, km 34	40.82556°N	3.43528°W	880 m	26-X-2006	GU06-01 – GU06-06
Loc. 16	SPAIN. Guadalajara: Usanos, road CM-1008, km 9	40.69889°N	3.24417°W	805 m	26-X-2006	GU06-07 - GU06-10
Loc. 17	SPAIN. Guadalajara: Sacedón, road CM-2000, km 55	40.46000°N	2.73167°W	765 m	26-X-2006	GU06-11 – GU06-16
Loc. 18	SPAIN. Guadalajara: Puebla de Don Francisco,	40.29000°N	2.76306°W	670 m	26-X-2006	CU06-01 – CU06-04
	road CM-2000, Jabalera					
Loc. 19	SPAIN. Guadalajara: Puebla de Don Francisco, road CM-2025, km 4	40.20167°N	2.73944°W	800 m	26-X-2006	CU06-05 - CU06-08
Loc. 20	SPAIN. Madrid: road M-512, km 21	40.41750°N	4.26389°W	787 m	19-II-2007	M07-01 - M07-10
Loc. 21	SPAIN. Madrid: road from Pelayos to San Martín de Valdeiglesias, path to Cerro Valdenoches, km 3	40.34028°N	4.36167°W	770 m	19-II-2007	M07-11 – M07-20
Loc. 22	SPAIN. Ávila: Fresnedilla	40.21056°N	4.64444°W	640 m	19-II-2007	AV07-01 - AV07-10
Loc. 23	SPAIN. Toledo: Real de San Vicente, road CM-5051, km 25	40.17056°N	4.66111°W	710 m	19-II-2007	TO07-01 - TO07-10
Loc. 24	SPAIN. Ávila: Gavilanes	40.27056°N	4.84500°W	680 m	19-II-2007	AV07-11 - AV07-20
Loc. 25	SPAIN. Toledo: Arenas de San Pedro, road from Ávila	40.11361°N	5.01194°W	530 m	19-II-2007	TO07-11 - TO07-20
	to Talavera de la Reina					
Loc. 26	SPAIN. Guadalajara: Aguilar de Anguita, road N-211, km 3	41.03944°N	2.41861°W	1162 m	9-VII-2007	GU07-01 – GU07-10
Loc. 27	SPAIN. Guadalajara: Turmiel, road CM-2107, km 8	41.01222°N	2.07556°W	1138 m	9-VII-2007	GU07-11 – GU07-20
Loc. 28	SPAIN. Teruel: Bañón, Puerto de Bañón	40.83278°N	1.17500°W	1227 m	9-VII-2007	TE07-19 - TE07-27
Loc. 29	SPAIN. Teruel: Mezquita de Jarque, Puerto del Esquinazo, road N-420, km 631	40.71528°N	0.89667°W	1425 m	9-VII-2007	TE07-28 – TE07-35
Loc. 30	SPAIN. Teruel: Castel de Cabra, Puerto de las Traviesas	40.80472°N	0.67083°W	1157 m	9-VII-2007	TE07-36 - TE07-42

APPENDIX 1 (Continuation).

	Locality	Coord	inates	Elevation	Sampling date	Voucher numbers
Loc. 31	SPAIN. Teruel: Alcañiz, road N-211, km 250	41.09333°N	0.14139°W	432 m	9-VII-2007	TE07-43 - TE07-52
Loc. 32	SPAIN. Zaragoza: Caspe, road Z-221, km 61	41.20750°N	0.02222°E	166 m	9-VII-2007	Z07-01 - Z07-10
Loc. 33	SPAIN. Zaragoza: Cuesta Falcón, road N-211, km 284	41.27333°N	0.04666°E	180 m	9-VII-2007	Z07-11 - Z07-20
Loc. 34	SPAIN. Zaragoza: Los Monegros, Caspe	41.36167°N	0.10472°W	335 m	9-VII-2007	Z07-21 - Z07-30
Loc. 35	SPAIN. Zaragoza: Bujaraloz, Sástago, Montes de la Retuerta, Laguna de la Playa	41.41139°N	0.14472°W	326 m	9-VII-2007	Z07-31 – Z07-38
Loc. 36	SPAIN. Huesca: Castejón de Monegros, Pallaruelo range	41.62083°N	0.20750°W	480 m	9-VII-2007	HU07-01 – HU07-10
Loc. 37	SPAIN. Huesca: Caldearenas, Puerto de Monrepos, road N-330, km 602	42.35361°N	0.39194°W	1312 m	9-VII-2007	HU07-11 – HU07-20
Loc. 38	SPAIN. Huesca: Sallent de Gállego	42.76222°N	0.33667°W	1350 m	9-VII-2007	HU07-22 – HU07-30
Loc. 39	SPAIN. Huesca: Lanuza, road A-136, km 16	42.75694°N	0.32083°W	1308 m	9-VII-2007	HU07-31 – HU07-40
Loc. 40	SPAIN. Huesca: Canfranc	42.69611°N	0.52917°W	1010 m	9-VII-2007	HU07-41 – HU07-48
Loc. 41	SPAIN. Huesca: Bordas de Lanuza, Tachera (Ansó-Zuriza)	42.85417°N		1287 m	9-VII-2007	HU07-49 – HU07-54
Loc. 42	SPAIN. Navarra: Isaba, road NA-2000, km 9	42.87556°N	0.82472°W	1215 m	10-VII-2007	NA07-01 – NA07-08
Loc. 43	SPAIN. Navarra: Yesa	42.61722°N	1.16000°W	810 m	10-VII-2007	NA07-09 – NA07-16
Loc. 44	SPAIN. Navarra: Caseda, San Zoilo chapel, road NA-534, km 19	42.50778°N	1.35083°W	518 m	10-VII-2007	NA07-17 – NA07-22
Loc. 45	SPAIN. Navarra: Masadas, road N-121, km 62	42.29861°N	1.65389°W	440 m	10-VII-2007	NA07-17 - NA07-22 NA07-23 - NA07-34
Loc. 45	SPAIN. Soria: Ólvega, path to Noviercas	41.75139°N	1.05585 W	1165 m		
Loc. 47	SPAIN. Soria: Almazán, road CL-101, km 86				10-VII-2007	SO07-01 – SO07-08
		41.39417°N	2.58500°W	1030 m	10-VII-2007	SO07-09 – SO07-16
Loc. 48	SPAIN. Soria: Rello, road SO-132, km 38	41.32222°N	2.74556°W	1110 m	10-VII-2007	SO07-17 – SO07-24
Loc. 49	SPAIN. Cuenca: Almonacid del Marquesado, road CM-310, km 5	39.86778°N	2.78222°W	763 m	10-V-2007	CU07-01 – CU07-10
Loc. 50	SPAIN. Cuenca: Motilla del Palancar, Cerros de la Rambla, road N-320, km 68	39.52806°N	1.89833°W	833 m	10-V-2007	CU07-11 – CU07-20
Loc. 51	SPAIN. Cuenca: La Pesquera-Enguidanos, path to Contreras dam	39.59028°N	1.56222°W	808 m	10-V-2007	CU07-21 – CU07-30
Loc. 52	SPAIN. Cuenca: Cepa, road CU-V-5009	39.72639°N	1.31833°W	1090 m	10-V-2007	CU07-31 – CU07-38
Loc. 53	SPAIN. Cuenca: road from Beteta to Masegosa	40.57194°N	2.06194°W	1310 m	10-V-2007	CU07-41 - CU07-50
Loc. 54	SPAIN. Teruel: Albarracín range, Bronchales-Pozondón	40.52250°N	1.56917°W	1489 m	10-V-2007	TE07-01 - TE07-08
Loc. 55	SPAIN. Teruel: road from Nogueras to Albarracín	40.43556°N	1.58444°W	1409 m	10-V-2007	TE07-09 - TE07-17
Loc. 56	SPAIN. Madrid: El Pardo, La Quinta palace	40.50167°N	3.74000°W	665 m	24-V-2006	M06-01 - M06-04
Loc. 57	SPAIN. Madrid: Miraflores de la Sierra	40.80500°N	3.77750°W	1085 m	24-V-2006	M06-05 - M06-12
Loc. 58	SPAIN. Madrid: Miraflores de la Sierra, road to Puerto de la Morcuera	40.83444°N	3.80056°W	1450 m	24-V-2006	M06-13 - M06-16
Loc. 59	SPAIN. Madrid: Puerto de la Morcuera	40.82750°N	3.83167°W	1800 m	24-V-2006	M06-17 - M06-20
Loc. 60	SPAIN. Madrid: El Escorial, road to Abantos	40.59972°N	4.16056°W	1215 m	24-V-2006	M06-21 - M06-24
Loc. 61	SPAIN. Madrid: El Escorial, Abantos	40.60417°N	4.17361°W	1540 m	24-V-2006	M06-25 – M06-28
Loc. 62	SPAIN. Orense: Rubiá, road N-120 to Biobra	42.47278°N	6.88750°W	460 m	3-VII-2006	006-01 – 006-02
Loc. 63	SPAIN. León: Balboa	42.69500°N	6.92889°W	665 m	4-VII-2006	LE06-01 – LE06-02
Loc. 64	SPAIN. Lugo: Os Ancares, road LU-1401	42.85889°N	6.88556°W	1075 m	4-VII-2006	LU06-01 – LU06-02
Loc. 65	SPAIN. Lugo: Castro, road LU-113	43.15722°N	7.47528°W	435 m	5-VII-2006	LU06-03 – LU06-04
Loc. 66	SPAIN. León: Riaño	42.99028°N	4.99500°W	1155 m	6-VII-2006	LE06-03 – LE06-04
Loc. 67	SPAIN. Palencia: Otero de Guardo	42.99028 N 42.90278°N	4.80083°W	1270 m	7-VII-2006	PA06-01 – PA06-02
Loc. 68	SPAIN. Almería: Níjar, San José, road AL-4200,	36.82778°N	2.03917°W	1270 m	1-I-2007	AL07-01 – AL07-02
	Mirador de las Amatistas					
Loc. 69	SPAIN. Soria: Navaleno, El Amogable	41.86000°N	2.94667°W	1148 m	2-XI-2006	SO06-01
Loc. 70	SPAIN. Soria: La Muedra, Cuerda del Pozo dam	41.85639°N	2.80944°W	1101 m	3-XI-2006	SO06-02
Loc. 71	SPAIN. Soria: Vinuesa, road from El Rayo to Sotillo del Rincón	41.92667°N	2.66000°W	1213 m	3-XI-2006	SO06-03
Loc. 72	SPAIN. Soria: San Leonardo de Yagüe	41.83611°N	3.04056°W	1055 m	4-XI-2006	SO06-04
Loc. 73	SPAIN. Gerona: Requesens, Roc Colom	42.44917°N	2.95556°E	461 m	2-IV-2008	GE08-01 – GE08-10
Loc. 74	SPAIN. Gerona: Santa Pau, Can Blanc, Fageda d'en Jordà	42.15000°N	2.52556°E	762 m	3-IV-2008	GE08-11 – GE08-20
Loc. 75	SPAIN. Cáceres: Peraleda de la Mata, road EX-118, km 57	39.82415°N	5.47966°W	332 m	21-IV-2009	CA09-01 - CA09-10
Loc. 76	SPAIN. Cáceres: Ibor, road EX-118, km 39	39.68413°N	5.45146°W	680 m	21-IV-2009	CA09-11 - CA09-20
Loc. 77	SPAIN. Cáceres: road EX-118, km 16	39.53715°N	5.37449°W	674 m	21-IV-2009	CA09-21 - CA09-30
Loc. 78	SPAIN. Cáceres: road EX-116 from Guadalupe to Villamayor, km 20	39.25938°N	5.39103°W	510 m	21-IV-2009	CA09-31 - CA09-40
Loc. 79	SPAIN. Badajoz: Quintana de la Serena, road EX-346, km 19	38.84668°N	5.73782°W	357 m	21-IV-2009	BA09-01 - BA09-10
Loc. 80	SPAIN. Badajoz: road EX-103 from Hira de la Serena to Llerena, km 115	38.61056°N	5.77551°W	520 m	21-IV-2009	BA09-11 – BA09-21
Loc. 81	SPAIN. Badajoz: Calera de León: Tentudía monastery, road BA-039, Km 8	38.05285°N	6.34216°W	1058 m	22-IV-2009	BA09-22 - BA09-30
Loc. 82	SPAIN. Huelva: Cañaveral de León: road HU-9108, km 1	38.01902°N	6.52817°W	582 m	22-IV-2009	H09-01 – H09-10
Loc. 82	SPAIN. Huelva: Canaveral de Leon. Toad no-9106, kill 1	37.92560°N	6.72140°W	560 m	22-IV-2009 22-IV-2009	H09-01 – H09-10 H09-11 – H09-20
Loc. 83	PORTUGAL, road IP-8 from Beja to Serpa	37.92560°N 37.92299°N	7.50581°W	220 m	22-IV-2009 22-IV-2009	PO09-01 – PO09-10
Loc. 85	PORTUGAL. Ourique, road IC-1 to Castro da Cola, Alcaria da Fernão,	37.57528°N	8.27965°W	198 m	22-IV-2009 22-IV-2009	PO09-11 – PO09-10
	2 km away from road N-1					
Loc. 86	PORTUGAL. São Bartolomeu de Messines, road IC-1, km 719	37.28218°N	8.28585°W	112 m	22-IV-2009	PO09-21 – PO09-30
Loc. 87	SPAIN. Huelva: San Silvestre de Guzmán, road A-499, km 21	37.41976°N	7.33106°W	142 m	23-IV-2009	H09-21 – H09-30
Loc. 88	SPAIN. Huelva: Punta Umbría, El Rápido	37.21355°N	7.02667°W	13 m	23-IV-2009	H09-31 - H09-33
Loc. 89	SPAIN. Huelva: Almonte, road A-486 to El Rocío, km 18	37.21001°N	6.50505°W	53 m	23-IV-2009	H09-34 - H09-36
Loc. 90	SPAIN. Sevilla: El Pedroso, Sierra Norte Natural Park, road A-432, Km 17	37.73501°N	5.82657°W	189 m	23-IV-2009	SE09-01 – SE09-10
Loc. 91	SPAIN. Sevilla: road A-455 from Conastantina to Lora del Río, km 32	37.78101°N	5.59635°W	370 m	24-IV-2009	SE09-11 - SE09-13
	SPAIN. Córdoba: Hornachuelos Mezquetillas de San Rafael	3/./9406°N	5.2/9949///	158 m	/4-IV-/IIII9	(()()9-()1 = (()()9-10
Loc. 92	SPAIN. Córdoba: Hornachuelos, Mezquetillas de San Rafael, road COR-530, km 9	37.79406°N	5.27994°W	158 m	24-IV-2009	CO09-01 – CO09-10

APPENDIX 1 (Continuation).

	Locality	Coordinates		Elevation	Sampling date	Voucher numbers
Loc. 94	SPAIN. Jaén: Quesada, Cazorla range, Prado de las Ubillas fountain	37.84107°N	2.98643°W	1454 m	24-IV-2009	J09-01 – J09-03
Loc. 95	PORTUGAL. Loulé, road to Quarteira CM-1297, km 2, close to the station	37.11524°N	8.05515°W	104 m	23-IV-2009	PO09-41 – PO09-42
Loc. 96	FRANCE. Font Romeu	42.50972°N	2.046111°E	1805 m	4-IV-2008	FR08-01 - FR08-10
Loc. 97	FRANCE. Mont-Louis	42.50917°N	2.125556°E	1541 m	4-IV-2008	FR08-11 – FR08-18

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