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What substrate cultures can reveal: Myxomycetes and myxomycete-like organisms from the Sultanate of Oman

Schnittler M[1], Novozhilov YK[2], Shadwick JDL[3], Spiegel FW[3], García-Carvajal E[4], König P[1]

[1]*Institute of Botany and Landscape Ecology, Ernst Moritz Arndt University Greifswald, Soldmannstr. 15, D-17487 Greifswald, Germany*
[2]*V.L. Komarov Botanical Institute of the Russian Academy of Sciences, Prof. Popov St. 2, 197376 St. Petersburg, Russia*
[3]*University of Arkansas, Department of Biological Sciences, SCEN 601, 1 University of Arkansas, Fayetteville, AR 72701, USA*
[4]*Royal Botanic Garden (CSIC), Plaza de Murillo, 2, Madrid, E-28014, Spain*

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Abstract

A total of 299 substrate samples collected throughout the Sultanate of Oman were analyzed for myxomycetes and myxomycete-like organisms (MMLO) with a combined approach, preparing one moist chamber culture and one agar culture for each sample. We recovered 8 forms of Myxobacteria, 2 sorocarpic amoebae (Acrasids), 19 known and 6 unknown taxa of protostelioid amoebae (Protostelids), and 50 species of Myxomycetes. Moist chambers and agar cultures completed each other. No method alone can detect the whole diversity of myxomycetes as the most species-rich group of MMLO. A significant overlap between the two methods was observed only for Myxobacteria and some myxomycetes with small sporocarps. Our results support the hypothesis that substrate cultures work best for arid study regions, but fail to recover a part of the species diversity in regions with a pronounced rainy season. From the three climatic regions of Oman, the northern mountainous region with a Mediterranean flora and climate had the highest diversity for MMLO (66 taxa from 943 records). The adjacent central desert, receiving only sporadic rain, was much poorer (29 taxa from 156 records). The Dhofar region with an east-African flora and a monsoon climate was intermediate in species richness (53 taxa from 249 records). For all three regions a significant proportion of the diversity (95, 82 and 86% of the taxa to be expected according to the Chao2 estimator) could be recovered. Fast developing MMLO with minute, stalked fruit bodies were especially common in the northern mountains, less in the Dhofar region, and nearly absent in the central desert where slow developing MMLO with larger, often sessile fruit bodies prevailed.

Key words – biodiversity – isolation – Myxobacteria – Myxogastria – protostelid amoebae – sorocarpic amoebae

Introduction

Slime molds (Myxogastria, commonly called myxomycetes and Dictyostelia, Adl et al. 2012) were treated as fungi until de Bary (1859, 1862) discovered the life cycle of myxomycetes,

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Corresponding Author: Martin Schnittler – e-mail – martin.schnittller@uni-greifswald.de

observing amoebae with or without flagella hatching from spores. From an ecological point of view, this treatment makes sense, since the fructifications usually disperse airborne spores like fungi. Ultrastructural and molecular investigations revealed that within different amoebal groups fructifications have been invented independently (Shadwick et al. 2009, Brown et al. 2012). This innovation seems to be linked to a predatory way of life, using the spores as propagules to exploit the rich microbial life in terrestrial habitat islands formed by decaying plant remnants. These organisms can be seen as an ecological guild of myxomycetes and myxomycete-like organisms (MMLO, Schnittler et al. 2006, 2012a). Unifying ecological traits are (i) living as predators of other microorganisms, (ii) starting their life cycle from meiotic or mitotic spores with (iii) obligate amoebae which (iv) later aggregate (sorocarpic) or grow into plasmodia by exclusively nuclear divisions (sporocarpic) to (v) convert this biomass to typically stalked fruit bodies which (vi) develop within hours not out of a true growth process but be rearrangement of the available biomass to (vii) release spores, most often adapted to aerial long-distance dispersal. These fruit bodies are primarily stalked (an ancestral character at least for myxomycetes, but the stalk may be secondary lost in many species, Fiore-Donno et al. 2009, 2010) and are 10 µm to 1 cm tall (compound fruit bodies in myxomycetes can be much larger but are usually not stalked). Fruit bodies are sometimes strikingly similar to those of microfungi and can be easily confused with them (Abdel-Raheem 2002).

Members of this guild are the prokaryotic myxobacteria (40–60 taxa, Reichenbach 1993, Garrity et al. 2004) developing fruit bodies up to 1 mm tall; plus a heterogeneous assemblage of protists, mostly members of the supergroup Amoebozoa (Eumycetozoa, compare Adl et al. 2012). Eumycetozoans as defined by Olive (1975) include myxomycetes, protostelids and dictyostelids (Fiore-Donno et al. 2005). The protostelids have been discovered late (Olive 1975, Spiegel 1990) since these amoebae form microscopic stalked fruit bodies 5–500 µm tall with usually one, rarely up to 8 spores on top. Formerly seen as ancestral to the myxomycetes, recent studies detected this group to be paraphyletic (Fiore-Donno et al. 2010, Shadwick et al. 2009). The most recent classification of Adl et al. (2012) distinguishes several main groups: Protosteliida, Cavosteliida, Protosporangiida (including the genus *Ceratiomyxa* traditionally treated as a myxomycete), Fractovitelliida and Schizoplasmodiida. Myxomycetes, excluding *Ceratiomyxa*, seem to be monophyletic as a group, and the same holds true for dictyostelids (Romeralo et al. 2011). The myxomycetes are the most species-rich group of eumycetozoans (ca. 940 taxa, Lado 2013), followed by dictyostelids (ca. 200 taxa, Cavender 1990, Romeralo et al. 2007) and protostelids (37 taxa described, Spiegel et al. 2007). Acrasid slime molds as treated by Olive (1975) and Blanton (1990) are clearly distant from all Eumycetozoa. Now better called sorocarpic amoebae, this group is paraphyletic as well and includes aggregating amoebae of different groups, even outside of Amoebozoa (Brown et al. 2009, 2010), like the genera *Acrasis*, *Pocheina* (Excavata: Heterolobosea, Adl et al. 2012), and *Fonticula* (Ophistokonta, Adl et al. 2012). Finally, the ciliate genus *Sorogena* (SAR: Ciliophora, Colpodea, Adl et al. 2012) develops fruiting bodies strikingly similar to those found in *Echinostelium* spp., a myxomycete genus (Bardele et al. 1991).

Since MMLO as an ecological guild are defined by ecological, not taxonomic, characters, their joint ecology should enable us to detect them as well in a joint approach. This was the first hypothesis to be tested in this survey, where we systematically used agar cultures to detect not only myxomycetes but also other taxa with microscopic fruit bodies. We second wanted to explore to which degree substrate cultures can detect a local community in dependence from aridity, testing the hypothesis that substrate cultures work best in arid regions. Third, we wanted to see if myxomycetes can manage to live in hyperarid regions with only sporadic rainfalls.

A student field trip to the Sultanate of Oman gave an opportunity to carry out a survey based primarily on substrate cultures. For myxomycetes it was shown in a series of surveys that moist chamber cultures are indispensable to recover the diverse biota in arid regions of Central Asia (Caspian Lowlands: Novozhilov et al. 2006, Western Kazakhstan: Schnittler & Novozhilov 2000; Innermountain basins of the Russian Altay: Novozhilov et al. 2009, Mongolia: Novozhilov &

Schnittler 2008, western China: Schnittler et al. 2012b). Such cultures performed also very well in the arid counterparts of the New World (Sonoran desert of Arizona: Evenson 1961, Blackwell & Gilbertson 1980, 1984; Colorado: Novozhilov et al. 2003; arid zones of Mexico: Estrada-Torres et al. 2005). Much less is known from Africa and in particular from the Arab Peninsula. The arid regions of Tanzania are relatively well studied (Ukkola 2005); from the Sahara desert a small data set is available (Faurel et al. 1965). The Sinai region and adjacent Israel is studied to some extent (Ramon 1968, Binyamini 1986, 1987, 1991). No systematic survey was carried out up to date for the Arab Peninsula; sporadic data we have from Yamamoto & Hagiwara (2003) for Saudi-Arabia. For the Sultanate of Oman, covering the three major climatic regions occurring in the Arab Peninsula, only a few taxa of dictyostelids have been described (Hagiwara 1991).

Materials & Methods

Study region: The Sultanate of Oman covers with 309 500 km^2 the southeastern corner of the Arabian Peninsula, including three distinctive climatic regions (Ghazanfar 1991a, Ghazanfar & Fisher 1998). The northeastern mountainous region (furthermore abbreviated as Mts.) consists of a narrow coastal plain (Batinah) with the capital Muscat, the Hajar Mountains with the highest summits of the country (Jebel Shams, 3009 m a.s.l.) and an inland foothill region. Whereas the coastal regions have a subtropical hot climate (annual mean temperature around Muscat 28 °C, mean precipitation 103 mm, Scholz 1999), the mountain region itself is characterized by a Mediterranean climate with higher precipitation (up to 350 mm per year) and climate with warm days but cool nights, allowing dew accumulation. The summit regions can have mild frost at night. In shrublands with scattered treelets we collected bark from *Acacia gerrardii* Benth. (Fabaceae), mainly in wadis (dry valleys), *Dodonaea viscosa* (L.) Jacq. (Sapindaceae), *Sideroxylon mascatense* (A. DC.) Penn. (Sapotaceae), *Olea europaea* L. subsp. *cuspidata* (Wall. ex G. Don) Cif. (Oleaceae) and *Juniperus excelsa* M. Bieb. subsp. *polycarpos* (K. Koch) Takhtajan (Cupressaceae), the latter forms savannah-like forests (10 –50 trees per hectare) with *Cymbopogon* spec. grasslands on the highest summit (Ghazanfar 1991b, Brinkmann et al. 2009).

The largest part of the country is occupied by the Central Desert region (Des.); here silty salt pans, stone deserts and sand dunes alternate. The driest part belongs to the Rub al Khali, the inland desert of the Arabian Peninsula. Only wadis and depressions with ground water access support solitary shrubs and treelets. We regularly sampled *Nannorrhops ritchieana* (Griff.) Aitch. (Arecaceae) in sand deserts, *Prosopis cineraria* (L.) Druce, *Acacia ehrenbergiana* Hayne and especially frequent *A. tortilis* (Forssk.) Hayne (all Fabaceae), but also some low shrubs, especially *Tetraena hamiensis* (Schweinf.) Beier et Thulin and *T. qatarensis* (Hadidi) Beier et Thulin (Zygophyllaceae). Rainfalls in this region occur sporadic; a given area can stay complete dry for several years.

Sharply distinct is the Dhofar region (Dho.) in the southwest: the coastal escarpment reaches up to 1000 m, with the highest summit at 1812 m, and catches monsoon clouds in a brief but intense rainy season lasting from beginning of July to mid September. Precipitation can reach more than 300 mm plus a fog equivalent estimated up to the double of that amount (Hildebrandt & Eltahir 2006). The steep south-facing slopes of the escarpment are covered by closed-canopy seasonal dry forests. We sampled the dominant tree species *Anogeissus dhofarica* A.J. Scott (Combretaceae), *Commiphora kua* (R. Br. ex Royle) Vollesen (Burseraceae), *Acacia etbaica* Schweinf. subsp. *uncinata* Brenan, *A. senegal* (L.) Willd., the shrub *Blepharispermum hirsutum* Oliv. (Asteraceae) and, in wadis, *Ziziphus spina-christi* (L.) Desf. (Rhamnaceae). The shallow north-facing slopes of the escarpment become drier and drier towards the north. Grasslands with scattered shrubs and treelets dominate; sampled were *Dracaena serrulata* Baker (Asparagaceae, formerly Dracaenaceae) but also *Solanum incanum* L. (Solanaceae). The famous frankincense tree (*Boswellia sacra* Flueck., Burseraceae) inhabiting these habitats was already too rare to be regularly sampled.

Our expedition was a three-week journey carried out from Feb. 6–28, 2005, describing a loop of about 2700 km that started and ended at the capital Muscat (Fig. 1). Substrata were sampled from altogether 70 localities (27 Mts., 27 Des., 16 Dho.) by the first and third author. Locality numbers used in the following list of localities are not consecutive, since at some localities only vascular plants but no myxomycete substrata were collected.

Mountain region (Mts.)

5: Batinah (Coastal Plain), *Muscat,* dry wadi bed with some *Acacia* trees 45 km W Muscat, Wadi Al Khad near the village Al Khad, 58°06'55"N, 23°33'41"E ± 50 m, 50 ± 20 m a.s.l., 8.2.2005; **5a:** dry wadi bed with a *Prosopis juliflora* stand, 58°06'51"N, 23°33'31"E ± 50 m, 50 ± 20 m a.s.l.; **5b:** side wadi with *Acacia tortilis* woodland, 58°06'24"N, 23°33'27"E ± 50 m, 112 ± 25 m a.s.l.; **6:** Hajar al Sharqui Mts., *Muscat,* Acacia woodland in the rubble fan of a wadi, 40 km SE Muscat (SE of Quriat), near village Hail Al Ghaf, branch of the road to Wadi Dayqah, 58°52'42"N, 23°12'15"E ± 25 m, 90 ± 10 m a.s.l., 9.2.2005; **7:** first right side wadi of the Wadi Dayqah, 58°55'45"N, 23°09'19"E ± 25 m, 105 ± 10 m a.s.l.; **8:** NE-exp., rocky slopes with scattered trees, Wadi Dayqah, ca. 4 km from its mound, 58°55'02"N, 23°08'22"E ± 25 m, 90 ± 10 m a.s.l., **8a:** upper rocky slopes with scattered shrubs, **8b:** SSW-exp., rocky slopes with scattered *Acacia* trees, **8c:** upper rocky slopes; **11:** Jebal Akhdar foothills, *Nizwa,* temporarily flooded flat wadi bed with some shrubs, 3 km W village Ghul, lowermost part of Wadi Ghul, 57°10'38"N, 23°09'17"E ± 50 m, 788 ± 50 m a.s.l., 10.2.2005; **11b:** gravelly flat wadi bed with some *Acacia* trees, not affected by floods; **11c:** gravelly flat wadi bed, successional stage after a flood; **12:** Jebal Akhdar Mts., *Nizwa,* steep, rocky, E-exp. slope of a small wadi, 10 km NE village Ghul, left of the access road to Jebal Shams, in a switchback of the road, 57°09'01"N, 23°12'43"E ± 50 m, 1380 ± 50 m a.s.l.; **13:** bedrock with some fine soil, scattered trees, 10 km N village Ghul, high plateau of Jebal Shams Mt., near the campground site, 57°12'06"N, 23°12'20"E ± 50 m, 1972 ± 50 m a.s.l.; **14:** right of the access road to Jebal Shams Mt., near Dar A' Sawda village, 57°11'59"N, 23°14'00"E ± 50 m, 1900 ± 50 m a.s.l., **14a:** W-exp- slope with some trees, boulders of a small wadi, right of the access road to Jebal Shams Mt., near Dar A' Sawda village, 57°11'59"N, 23°14'00"E ± 50 m, 1900 ± 50 m a.s.l.; **14b:** NW-exp- slope with some trees, bedrock with some finer soil, right of the access road to Jebal Shams Mt., near Dar A' Sawda village, 57°11'59"N, 23°14'00"E ± 150 m, 1920 ± 50 m a.s.l.; **15:** shallow NW-exp- slope with some trees, bedrock with some finer soil, left of the access road to Jebal Shams Mt., near the plateau, 57°12'16"N, 23°13'34"E ± 50 m, 1958 ± 50 m a.s.l.; **16:** Jebal Akhdar Mts., *Nizwa,* shallow E-exp. wadi bed, bedrock with finer soil and boulders, ca. 50 m N of trailhead to Jebal Shams summit trail from the access road, 57°12'32"N, 23°13'30"E ± 50 m, 1957 ± 50 m a.s.l., 11.2.2005; **17:** shallow NW-exp. slope, bedrock and boulders, Jebal Shams summit trail, ca. 3 km from trailhead, 57°13'07"N, 23°13'23"E ± 50 m, 1963 ± 50 m a.s.l.; **18:** shallow SW-exp. slope, bedrock and boulders, Jebal Shams summit trail, near the cliffs to Wadi Ghul ("Grand Canyon"), 57°13'81"N, 23°13'57"E ± 50 m, 2240 ± 50 m a.s.l.; **19:** shallow W-exp. slope, bedrock and boulders, 57°14'29"N, 23°13'49"E ± 50 m, 2428 ± 50 m a.s.l.; **20:** NNE-exp. grassy slope, *Juniperus*-dominated woodland on finer soil over bedrock, 57°14'34"N, 23°13'49"E ± 50 m, 2400 ± 50 m a.s.l.; **22:** steep W-exp. wadi, boulders, some shrubs and trees, 8 km N village Ghul, left of the access road to Jebal Shams Mt., 57°10'27"N, 23°14'39"E ± 50 m, 1683 ± 50 m a.s.l.; **24:** stony SSE-exp. wadi bed, large boulders, 1 km N village Ghul, in the switchbacks of the access road to Jebal Shams Mt., 57°08'58"N, 23°12'10"E ± 50 m, 1207 ± 50 m a.s.l.; **24a:** stony E-exp. wadi bed, side wadi of the Wadi Ghul, 1 km N village Ghul, left of the access road to Jebal Shams Mt., 57°08'25"N, 23°11'12"E ± 50 m, 970 ± 50 m a.s.l.; **80:** Hajan Al-Sharqui foothills, *Ibra,* wadi bed near a well, heavily browsed, 5 km E Al-Mazryah, along the road to Ibra, 58°27'30"N, 22°47'48"E ± 25 m, 533 ± 25 m a.s.l., 25.2.2005

Desert region (Des.)

25: Rub Al Khali, *Nizwa,* sandy desert with scattered *Acacia* trees, 60 km S Nizwa, ca. 500 m left of road 31 (Nizwa to Salalah), 57°31'01"N, 22°16'53"E ± 50 m, 270 ± 25 m a.s.l., 13.2.2005; **26:** sandy desert, shallow depression with a group of *Acacia* trees, 100 km S Nizwa, ca. 500 m right of road 31 (Nizwa to Salalah), 2.5 km WSW of a cell phone tower, 57°27'48"N, 21°57'34"E ± 50 m, 230 ± 25 m a.s.l.; **27:** sandy desert, shallow depression with a group of *Acacia* trees, 120 km S Nizwa, ca. 500 m left of road 31 (Nizwa to Salalah), 57°20'52"N, 21°47'07"E ± 50 m, 184 ± 25 m a.s.l.; **28:** *Adam,* sandy desert, shallow wadi with dwarf palms, 90 km S Adam, ca. 500 m right of road 31 (Nizwa to Salalah), 57°22'49"N, 21°49'35"E ± 50 m, 200 ± 25 m a.s.l., 14.2.2005; **28a:** sandy desert, near a shallow wadi, desert shrub community; **29:** bed of a shallow wadi, dwarf palm and *Acacia* trees, 95 km S Adam, ca. 3 km right of road 31, 57°18'27"N, 21°43'45"E ± 50 m, 183 ± 25 m a.s.l.; **30:** *Adam,* plain sandy desert with some *Acacia* shrub, 270 km S Adam (near Hajma), ca. 500 m right of road 31, 56°58'16"N,

20°34'21"E ± 50 m, 134 ± 25 m a.s.l.; **31:** *Haima,* plain gravel desert with some low shrub, 455 km N Salalah (near Hajma), ca. 500 m right of road 31, 56°05'19"N, 19°44'06"E ± 50 m, 153 ± 25 m a.s.l.; **32:** plain gravel desert with some low shrub, 440 km N Salalah, ca. 500 m right of road 31, 55°57'14"N, 19°44'06"E ± 50 m, 176 ± 25 m a.s.l.; **33:** plain gravel desert with some low shrub, 418 km N Salalah, ca. 500 m right of road 31, 55°45'07"N, 19°37'03"E ± 50 m, 173 ± 25 m a.s.l.; **40:** sand dunes over gypsum stones 370 km N Salalah, ca. 500 m right of road 31, 55°23'05"N, 19°36'23"E ± 50 m, 136 ± 25 m a.s.l.; **41:** *Dauka,* sandy wadi bed with some *Prosopis* trees 125 km N Dauka, ca. 200 m right of road 31, 54°49'58"N, 19°29'19"E ± 50 m, 120 ± 25 m a.s.l.; **42:** *Dauka,* totally flat sand-gypsum desert, 35 km N Dauka, ca. 300 m left of road 31, 54°17'58"N, 18°53'37"E ± 50 m, 191 ± 25 m a.s.l., 15.2.2005; **46:** *Shisr, Acacia* shrub in a shallow depression, sand-gravel desert 30 km SSE Shisr, at the gravel road from road 31to Shisr, 53°47'35"N, 17°54'02"E ± 50 m, 391 ± 25 m a.s.l.; **47:** *Acacia* shrub in a wadi, sand-gravel desert 50 km SSE Shisr, at the gravel road from road 31 to Shisr, 53°56'19"N, 17°47'54"E ± 50 m, 415 ± 25 m a.s.l.; **68:** *Hajma,* plain sand-gypsum desert 20 km N Hajma, ca. 500 m N of the road from Hajma to Al Duqm 56°24'28"N, 19°57'05"E ± 50 m, 169 ± 25 m a.s.l., 21.2.2005; **70:** Coastal desert, *Al Duqm,* wadi bed with *Acacia* and *Prosopis* trees, fine sand over gypsum bedrock, 5 km SSW Al Duqm (fish processing plant), ca. 3 km away from the sea, 57°40'55"N, 19°37'24"E ± 25 m, 28 ± 0 m a.s.l., 22.2.2005; **71:** wadi bed with *Acacia* and *Prosopis* trees, fine sand over gypsum bedrock 8 km SSW Al Duqm, ca. 4 km away from the sea, right off the gravel road connecting the village with the coastal road, 57°39'53"N, 19°36'14"E ± 25 m, 38 ± 0 m a.s.l.; **73:** *Sanaw,* grazed *Prosopis* parkland in a depression, fine sandy soil, 120 km N Sanaw, near the road to Ibra, 58°14'58"N, 21°27'54"E ± 25 m, 105 ± 25 m a.s.l., 23.2.2005; **75a:** Wahiba Sands, *Ibra,* sand dunes 600 m SE Al-Hawaiyah oasis, near Al Mintirib, 58°51'42"N, 22°23'04"E ± 50 m, 312 ± 50 m a.s.l.; **75b:** sand dunes 1 km SE Al-Hawaiyah oasis, 58°51'52"N, 22°22'57"E ± 50 m, 320 ± 50 m a.s.l.; **76:** severely overgrazed *Acacia* woodland in a wadi bed, rubble overcast with sand, 1 km NE of the road from Sanaw to Ibra,, 58°57'28"N, 22°30'41"E ± 25 m, 350 ± 25 m a.s.l.; **76a:** shrubland in a wadi bed, rubble fan of the mountain foothills; **77:** large sand dunes 2.5 km SSW Al Wasil oasis, near Al Mintirib, 58°44'25"N, 22°28'51"E ± 25 m, 377 ± 50 m a.s.l., 24.2.2005; **77a:** large sand dunes 2.7 km SSW Al Wasil oasis; 58°44'19"N, 22°28'43"E ± 25 m, 377 ± 50 m a.s.l.; **79:** Hajan Al-Sharqui foothills, *Ibra,* sandy wadi bed, 120 km SE Ibra, along the road from Bani Bu Hassan to the coast 59°15'48"N, 22°08'04"E ± 25 m, 147 ± 25 m a.s.l., 25.2.2005

Dhofar region (Dho.)

48: Jebal Qara, *Salalah,* stony cow pasture on the escarpment plateau 30 km N Salalah, right off the road 31 (Nizwa to Salalah) 54°05'52"N, 17°12'53"E ± 50 m, 724 ± 25 m a.s.l., 16.2.2005; **50:** Jebal Samhan, *Salalah,* small SSE-exp. ravine with *Anogeissus* woodland 10 km N Taqah, left of the pass road to Tawi Attair, environs of Wadi Darbat 54°27'11"N, 17°04'15"E ± 25 m, 316 ± 25 m a.s.l., 17.2.2005; **51:** S-exp. ravine with *Commiphora* dry scrubland, 8 km N Taqah, 54°26'52"N, 17°03'57"E ± 25 m, 146 ± 25 m a.s.l.; **52:** shallow NW-exp. wadi with *Anogeissus* woodland 12 km N Taqah, right of the pass road to Tawi Attair, 54°27'19"N, 17°04'05"E ± 25 m, 314 ± 25 m a.s.l.; **53:** Coastal Plain, *Salalah,* stony cow pastures, 5 km ENE Taqah, left of the road from Sallato to Tawi Attair, environs of Wadi Darbat 54°24'42"N, 17°03'11"E ± 25 m, 56 ± 20 m a.s.l.; **54:** Jebal Qamar, *Salalah,* stony shrubland, E-exp. slope on limestone 10 km W Mughsayl, right off the road from Salalah to Sarfait 53°45'29"N, 16°52'31"E ± 25 m, 204 ± 25 m a.s.l., 18.2.2005; **55:** steep SE-exp. slope with *Dracena* trees ca. 2 km from the seashore, 110 km W Salalah, right off the road from Salalah to Sarfait (ca. 5 km before the army checkpoint), 53°40'31"N, 16°49'40"E ± 25 m, 851 ± 25 m a.s.l.; **56:** stony cow pastures, 120 km W Salalah, right off the road from Salalah to Sarfait (ca. 8 km beyond the army checkpoint), 53°35'17"N, 16°47'22"E ± 25 m, 1028 ± 25 m a.s.l.; **57:** *Anogeissus* woodland at a shallow SW-exp. slope 130 km W Salalah, left off the road from the escarpment to Rakhyut 53°19'55"N, 16°47'10"E ± 25 m, 879 ± 25 m a.s.l.; **58:** *Anogeissus* woodland in a NE-exp. ravine 130 km W Salalah, switchbacks of the road from the escarpment to Rakhyut 53°24'53"N, 16°44'38"E ± 25 m, 135 ± 25 m a.s.l.; **59:** Jebal Qamar, *Salalah, Commiphora-Anogeissus* woodland in a dry NE-exp. slope 130 km W Salalah, right off the road from the escarpment to Rakhyut 53°24'50"N, 16°44'32"E ± 25 m, 182 ± 25 m a.s.l.; **61:** Jebal Qara, *Salalah,* steep, S-exp. rocky wadi 15 km N Salalah, pass road to Garziz and Ittin, left off the road 54°04'51"N, 17°06'15"E ± 5 km, 340 ± 25 m a.s.l., 19.2.2005; **62:** steep NE-exp. slopes of a large wadi 3 km SW Ain Garziz, 54°03'45"N, 17°06'29"E ± 50 m, 306 ± 50 m a.s.l.; **62a:** steep

NE-exp. slopes of the large wadi, small drier ridge, 54°03'44"N, 17°06'35"E ± 50 m, 268 ± 50 m a.s.l.; **63:** sandy bottom of the large wadi, near the slope 54°03'50"N, 17°06'38"E ± 50 m, 172 ± 50 m a.s.l.; **67:** Jebal Samhan, *Salalah, Anogeissus* stands on steep slopes of a carstic sinkhole, 40 km ENE Salalah, Tawi Attair sinkhole 54°33'52"N, 17°06'38"E ± 50 m, 17 ± 10 m a.s.l., 20.2.2005

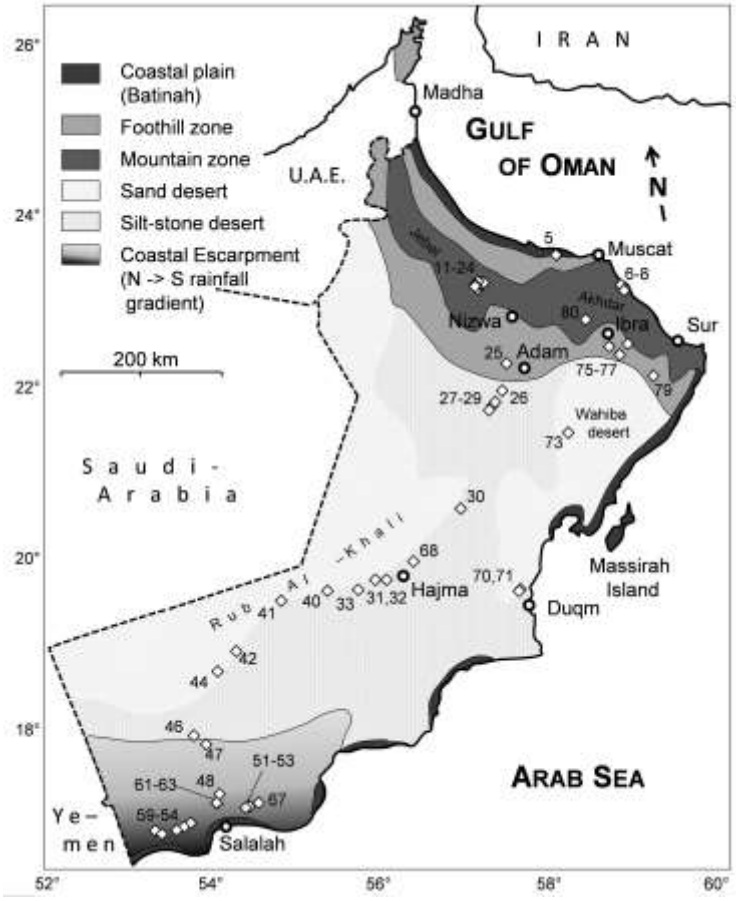

Fig. 1 – Sampled localities (diamonds) and natural regions of Oman (modified after Scholz 1999). For locality numbers compare text.

Substrata sampling: Four main groups of substrata were sampled for the present study in all major biomes of the country: (b) dead outer part of the bark from larger living shrubs or trees, (w) small, slowly decaying twigs and branches of trees and shrubs on ground, usually decorticated, (l) thin mats of litter at the base of trees or shrubs, and (d) dung of herbivorous animals. Substrata were collected in 2–3 pieces of from 5 to 10 plant individuals or points within a vegetation unit (usually a plot of 50 x 50 m), sharing the same microhabitat features. These were pooled, yielding a total sample weight of 15–25 g. Bark of living plants was further subdivided into "texture groups" according to its physical features (Schnittler 2001). These were smooth bark (b1, *Tetraena* spp.), smooth bark with some isolated flakes rolling outwards (b2, *Tamarix* spp.), peeling in long, more or less loose strips and in older trunks of *Juniperus* often forming a sheath of 2–5 layers (b3, *Juniperus excelsa*, *Calligonum* spp., *Commiphora* spp.); solid and deeply furrowed bark (b4, *Anogeissus dhofarica*, *Sideroxylon mascatense*, *Olea europaea*, *Ziziphus spina-cristi*, old trunks of all Fabaceae trees); finally fibrous bark of *Fagonia indica* Burm. f. (Zygophyllaceae). Litter was classified into leafy ground litter (ll), consisting of decaying leaves forming mats 0.5–2 cm thick beneath shrubs and trees, aerial herbaceous litter (lh) of dead inflorescences of larger plants (e.g., *Blepharospermum*, *Dracaena*, *Nannorrhops*) and grass litter (lg) sampled from various grass species in grasslands, especially *Cymbopogon* spp. Twigs of sufficient size to be easily noticed in the field were selectively excluded from all litter samples but sampled separately as decayed wood (w, classified into three stages of decay). Partially decomposed droppings of herbivores (d) were represented by various wild rodents 0.5–1 cm diam.; sheep 0.8–1.5 cm diam.; donkey and camel 2.5–5 cm diam., and, exclusively in the Dhofar region, cattle and horse; both 4–20 cm in diam.

From each of the 299 substrate samples one moist chamber culture was prepared with distilled water, using three layers of white toilette paper in Petri dishes (9 cm diam.). The whole area (app. 60 cm^2 of a Petri dish was tightly covered with substrate pieces, for larger bark flakes the outer site was placed up. After approximately 24 h, excess water was poured off and pH values were determined at three points of the wet substratum surface using an Orion model 610 pH meter with a touch down probe. Cultures were incubated under ambient light and at room temperature (ca 20–24 °C) for up to 90 days and scanned for myxomycetes on four occasions (days 6, 11, 21, 40) using a Semi SV11 (Zeiss) dissecting microscope. Large colonies of protostelids were frequently seen but could not be determined with a dissecting microscope.

In a similar way, agar cultures were prepared, using about 0.5–2 g of dry material per sample arranged into four streaks, each consisting of 3–6 substratum pieces 1–2 mm in size. Using sterile tweezers, substratum pieces were placed on a weak malt yeast agar (0.002 g malt extract, 0.002 g yeast extract, 0.75 g potassium hydrogen phosphate, and 15 g agar/L distilled water) poured 3–5 mm deep in Petri dishes of 9 cm diameter. All agar cultures were maintained at room temperature (20–24 °C) and checked at six occasions (days 3, 5, 8–9, 13, 21, at the latter two dates only for myxomycetes) using the 10x and 20x objectives of a compound microscope, for larger fructifications the dissecting microscope was used. The entire margin of a substratum piece and the surrounding agar surface was systematically scanned for the presence of MMLO fructifications.

Herein, a record is defined as a colony of fructifications from one taxon developing in a culture. If a taxon appeared in both moist chamber and in agar culture made from the same substrate collection, it was counted as a single record.

Species determination and annotated species list: Myxomycetes were determined according to standard literature (see also the webpage of the Eumycetozoan project, 2010). Protostelid taxa were keyed out according to Spiegel et al. (2007). For both groups, nomenclature follows Lado (2013). Although the trophic cells of protostelids are quite diverse (Olive 1975, Spiegel & Feldman 1985), they are hard to spot on agar and can easily be confused with that of other free-living amoebae. Therefore, as for myxomycetes diagnostic characters are mostly those of the fructification, like length and thickness of the stalk and stalk tip, spore attachment and spore shape (Spiegel et al. 2007). For myxobacteria recent literature is rare, tentative determinations were made according to Reichenbach (1993); nomenclature follows Bergey's taxonomic outline (Garrity et al. 2004).

For determination, sporocarps of myxomycetes, and, if manageable, protostelids were preserved as permanent slides in lactophenol, and Hoyer's medium and/or glycerol gelatine were used to distinguish between limeless and lime-containing structures. Standard color notations are given in parentheses according to ISCC-NBS Color-Name Charts illustrated with centroid colors (Anonymus 1976). Sporocarp structures were studied with a JEOL 35c scanning electron microscope (SEM) at St. Petersburg. Voucher specimens are deposited in the Komarov Botanical Institute of the Russian Academy of Sciences, Laboratory of Systematics and Geography of Fungi (LE), with duplicates in the Botanical State Collection Munich (M).

Data evaluation: Species accumulation curves were constructed according to the rarefaction formula using the program EstimateS (Version 7, Colwell 2004, 50 randomizations), which computes also a number of estimators of species richness. In accordance with Unterseher et al. (2008), the Chao2 estimator was chosen as the best estimator and calculated with the "classical settings" of estimateS. In addition, a hyperbolic regression according to the Michaelis-Menten formula $y = ax/(b+x)$, resulting in a curve shape coming very close to a broken-stick model (Magurran 2004,compare Schnittler 2001) was applied to the data, with the parameter *a* giving an estimate for the maximum number of species to be expected at this kind of substrate.

Species diversity (alpha-diversity) for the natural regions of Oman was calculated using Shannon's diversity index $H' = -\sum P_i \log P_i$, where P_i is the relative abundance (here the proportion of the total number of records represented by species) of a particular species (Shannon & Weaver 1963, Magurran 2004); Simpson's dominance index as $D = \sum P_i^2$. The Søerensen coefficient for a comparison of the regional communities was computed as $SC = 2c / (a + b + c)$ with a and b as the number of species exclusively to one community and c as the number of species shared by both communities.

Results

Annotated species list. The total of moist chamber and agar cultures for each of the 299 substrate samples yielded 1348 records from 85 taxa of MMLO, including 8 forms of myxobacteria (four of these could not be assigned to a taxon), 2 sorocarpic amoebae, 25 protostelids (six of these represented unknown forms), and 51 myxomycetes (with one form of *Didymium* that could not be assigned to a known species). Exclusively in the Dhofar region we found another 12 field collections, apparently all developed during the previous rainy season, representing another 2 myxomycete species not recorded from substrate cultures.

In the following annotated species list, determinations based on well-developed specimens that could not be assigned to a known species without doubt are denoted as "cf." (confer), those represented by very scanty or mal developed specimens only are indicated by (?). After each name, an estimation of abundance as described by Stephenson et al. (1993) is given in brackets, followed by the total number of records (for this purpose, a species harvested from one substrate collection represents one record, even it was found in both moist chamber and agar culture). This is based upon the proportion of a species to the total number of records for each group (51 for Acrasiid amoebae, 134 for myxobacteria, 485 for protostelids, 678 for myxomycetes): **R** – rare (< 0.5 %, 6 records), **O** – occasional (> 0.5–1.5 %, 7–18 records), **C** – common (> 1.5–3 %, 19–35 records), **A** – abundant (> 3 %, more than 35 records). Due to the rarity of field collections, this scale was applied to moist chamber collections only. Field collections (12 records from eight species) are listed with + and its number for the respective regions, but were omitted from all other evaluations.
With the denominators Mts. (mountain region), Des. (central desert region) and Dho. (Dhofar) the number of records from the three climatic regions are indicated, and after a slash in a similar way the records made on the four main substrata types, symbolized by b (bark of living trees and shrubs), d (herbivore dung), l (litter) and w (decayed wood). After a second slash the numbers of records observed in moist chamber cultures (mc), agar cultures (ag) or in the field (fc) are listed. Their sum is usually larger than the sum of records per sample as often a species appeared in both the moist chamber and the agar culture of a substrate sample. In parentheses, the mean development time for a species in moist chamber / agar culture is given. Selected vouchers are cited with a prefix denoting the herbarium in which the specimen is deposited plus the respective accession number. The string "…" indicates species with additional collections.

Myxobacteria

Chondromyces crocatus Berkeley & Curtis 1874 [C, 4] Mts: 4 / b: 1 d: 2 l: 1 / mc: 4, ag: 0 (21.0/- days)
One of the few morphologically distinctive myxobacteria; rather tall, orange (v.O 48) solitary sporangia with pointed sporangioles on a slender (White 263) stalk. Fructifications up to 800 µm tall on a slender stalk, more common in tropical areas.

***Nannocystis* spec. A** [A, 42] Mts: 27 Des: 13 Dho: 2 / b: 6 d: 8 l: 9 w: 19 / mc: 25, ag: 24 (18.3/6.1 days), 23396,…

***Nannocystis* spec. B** [C, 3] Des: 3 / w: 3 / mc: 0, ag: 3 (-/6.0 days)
Both species have vermicular sessile fructifications of irregular shape with a leathery, dark orange (deep O 51) peridium, often appearing coprophilous; for spec A. they are up to 300 µm in size, for spec. B below 120 µm.

Melittangium lichenicola (Thaxter 1892) McCurdy 1971 [A, 30] Mts: 15 Des: 3 Dho: 12 / b: 18 l: 8 w: 4 / mc: 6, ag: 25 (8.5/6.4 days), 23243,…
The most common myxobacterium in most survey, very distinctive by its gregarious, often large colonies of short stalked fructifications ca. 100 µm tall. The stout stalk is whitish (White 263) and well separated from the elliptical, orange-red (v.O 48 to s.O 50) sporangiole.

Myxococcus cf. ***xanthus*** Beebe 1941 [A, 14] Mts: 7 Des: 4 Dho: 3 / b: 1 d: 10 l: 2 w: 1 / mc: 6, ag: 8 (27.7/5.9 days), 23321,…
A common myxobacterium occurring in most surveys including moist chamber cultures throughout the world, with cream (yWhite 92) to yellowish (p.OY 73), but mostly pink (l.yPk 28) sessile fructifications with a shining, slimy surface quite variable in size within one colony. The morphospecies as recognized here is probably a whole complex of related strains difficult to tell apart by morphology only.

Stigmatella aurantiaca Berkeley & Curtis 1875 [A, 13] Mts: 12 Dho: 1 / b: 7 d: 1 l: 5 / mc: 13, ag: 1 (16.3/8.0 days), 23236,…
Common in temperate and tropical zones; branched, golden-brown (s.O 50 to deep O 51), grape-like groups of sporangioles on a joint, up to 700 µm tall stalk.

Stigmatella spec. [A, 8] Mts: 8 / d: 3 l: 5 / mc: 6, ag: 2 (40.0/6.5 days), see sc23414
Similar to *Stigmatella aurantiaca*, but nearly sessile, it may be only a stout form of this species.

Myxobacterium *spec. div.* [A, 20] Mts: 13 Dho: 7 / b: 15 l: 5 / mc: 0, ag: 20 (-/7.9 days)
Very small myxobacterium fructifications from agar cultures which could not even tentatively determined due to time constraints, at least some of these may be mal developed *Mellitangium lichenicola*.

Sorocarpic amoebae

Acrasis cf. ***rosea*** Olive & Stoian. [–, 2] Mts: 2 / b: 2 / mc: 0, ag 2, (-/5.5 days)
Long-stalked sorocarps with several branched chains of pinkish (l.yPk 28 to p.yPk 31), nearly translucent spores. The richly branched spore chains with about 15 spores are more typical for *A. helenhemmesae*, a species meanwhile described as new from isolates formerly assigned to *A. rosea* (Brown et al. 2010).

Copromyxa cf. ***protea*** (Fayod) Zopf [A, 49] Mts: 42 Des: 2 Dho: 5 / b: 22 d: 1 l: 24 w: 2 / mc: 17, ag: 37
A very small acrasid with small fructifications (50–70 µm in diam.) of irregular shape, often protruding like several fingers from the substrate surface, usually translucent or with slight pinkish hues (p.yPk 31), often in large colonies on bark.

Protostelid amoebae (all records from agar cultures)
Cavostelium apophysatum Olive [A, 68] Mts: 55 Des: 3 Dho: 10 / b: 54 d: 2 l: 8 w: 4 (5.5 days)
A short-stalked protostelid more common in tropical regions.

Microglomus paxillus Olive & Stoian. [A, 23] Mts: 19 Dho: 4 / b: 22 l: 1 (6.6 days)
A rare protostelid, short stalked, the several spores in a sporangium are often hard to see since they are hygroscopic and appear as a round water drop.

Nematostelium gracile (Olive & Stoian.) Olive & Stoian. [A, 25] Mts: 14 Dho: 11 / b: 6 d: 2 l: 17 (5.9 days)
One of the most easy to detect protostelids; a single spore on an up to 500 µm long stalk.

Nematostelium ovatum (Olive & Stoian.) Olive & Stoian. [C, 11] Mts: 9 Dho: 2 / l: 11 (5.8 days)
Similar to the previous species, but spores markedly ovoid.

Planoprotostelium cf. ***aurantiacum*** Olive & Stoian. [R, 1] Mts: 1 / l: 1 (5.0 days)
Very similar to *P. mycophaga*, but spores not deciduous, remaining on the stalk.

Protostelium arachisporum Olive [O, 5] Mts: 2 Dho: 3 / b: 3 l: 1 w: 1 (5.6 days)
Distinctive by its irregularly to angular shaped, large spore. The species may be more abundant in tropical regions.

Protosporangium articulatum Olive & Stoian. [A, 52] Mts: 41 Des: 8 Dho: 3 / b: 52 (5.7 days)
Stalk larger, 70–90(110) µm long, usually sharply bent and very thin towards the apex, thus the spore ball consisting of usually 4 spores waves with the slightest breeze, making the often large colonies easy to detect.

Protosporangium conicum Bennett [A, 39] Mts: 35 Des: 2 Dho: 2 / b: 39 (5.4 days)
Smaller than the previous species, with a 40–50 µm long stalk and (2)3–4 spores, the lower one often conical, letting the sporangium appear to be pear-shaped. This and the previous species are reported as rare, but our study revealed that they are strictly limited to bark, and thus most likely escaped detection in most protostelid surveys using litter substrates.

Protostelium mycophaga Olive & Stoian. [A, 25] Mts: 12 Dho: 13 / b: 8 l: 17 (5.7 days)
The most common protostelid in temperate zones, the irregularly bent stalks appearing "crooky" are very distinctive even if the spores of this deciduous species fell down, they can later often be detected on the agar surface near the stalk.

Protosteliopsis fimicola (Olive) Olive & Stoian. [O, 7] Mts: 4 Dho: 3 / d: 7 (5.6 days)
As described for the species, it was found on dung.

Protostelium nocturnum Spiegel [O, 5] Dho: 5 / l: 5 (4.4 days)
Another ballistosporous species, but in contrast to *P. mycophaga* the stalk disappears at spore dispersal, smaller than this species.

Schizoplasmodium cavostelioides Olive & Stoian. [O, 4] Dho: 4 / l: 4
A short stalked but ballistosporous species (usually this character is connected with long stalks).

Schizoplasmodiopsis micropunctata Olive & Stoian. [R, 1] Dho: 1 / b: 1 (6.2 days)
Rare, similar to *Tychosporium*, but stalk with an extremely thin, nearly invisible apex.

Schizoplasmodiopsis amoeboidea Olive & Whitney [A, 61] Mts: 49 Des: 2 Dho: 10 / b: 44 l: 17 (5.5 days)
A large but short stalked protostelid with spherical spores up to 15 µm in diameter. Common in most protostelid surveys.

Schizoplasmodiopsis pseudoendospora Olive, Martin & Stoian. [A, 57] Mts: 45 Des: 1 Dho: 11 / b: 40 d: 1 l: 16 (5.8 days)
Smaller than the previous species and extremely common on bark, often forming large colonies of gregarious sporocarps, which can be detected even in moist chamber cultures during the first days by two features: first, the single spores appear brilliant shining, and second the whole fructification often detaches from the substrate and floats freely on a water film covering the substrate, with fructifications still upright due to a enlarged, disk-like base of the stout stalk.

Schizoplasmodiopsis vulgare Olive & Stoian. [C, 14] Mts: 12 Dho: 2 / b: 10 l: 4 (5.8 days)
A long-stalked species with deciduous spores, usually very common but fairly rare in this survey.

Soliformovum expulsum (Olive & Stoian.) Spiegel [O, 6] Mts: 3 Dho: 3 / l: 6 (5.7 days)
A ballistosporius species with a moderately long stalk, distinctive prespore cells with a well visible nucleus–like inner area ("fried-egg" stage, Spiegel et al. 2007). As in *P. nocturnum*, with spore dispersal the stalk disappears as well.

Soliformovum irregularis (Olive & Stoian.) Spiegel [O, 6] Mts: 4 Dho: 2 / b: 2 l: 4 (6.8 days)
A long staked species, deciduous species with a spindle-shaped thickening (apophysis) at the stalk apex, spores often quickly shrinking due to dessication during observation of an open Petri dish.

Tychosporium acutostipes Spiegel, Moore & Feldman [O, 7] Dho: 7 / b: 1 l: 5 w: 1 (6.3 days)
A long stalked species with a pointed stalk, but apex not hair-like as in *S. micropunctata*. Reported with a preference for aquatic habitats, in this survey found only in the Dhofar region.

The following six forms of protostelids may represent non-described taxa; we at least could not assign them to described species without doubt. Since the Hajar mountains are very rich in protostelids, a detailed study including attempts to obtain pure cultures of the species seems to be desirable.

Protostelid spec. A [A, 19] Mts: 17 Des: 1 Dho: 1 / b: 19 (5.7 days), Fig. 2a.
Similar to *Schizoplasmodiopsis amoeboidea* but stalk more stout, not tapering into a thinner tip.

Protostelid spec. B [C, 13] Mts: 13 / b: 13 (5.7 days), Fig. 2b.
Similar to *Schizoplasmodiopsis amoeboidea* but stalk extremely stout and conical. This and the previous form may be within the variability of *S. amoeboidea*, a species which is common and widespread.

Protostelid spec. C [C, 13] Mts: 12 Dho: 1 / b: 13 (5.3 days), Fig. 2c.
Similar to *Schizoplasmodiopsis pseudoendospora* but with a very long, slender stalk, nearly three times as long as the spore.

Protostelid spec. D [A, 19] Mts: 18 Des: 1 / b: 19 (5.7 days), Fig. 2d, e.
Fructifications with a single large spore with articulate surface (similar to that of *Echinostelium colliculosum*); deciduous but not ballistosporous; the spore usually slides down the stalk on a water drop. ***Protostelid*** spec. E [O, 3] Mts: 3 / b: 3 (8.0 days)

Protostelid spec. F [R, 1] Mts: 1 / b: 1 (8.0 days)
Fructifications with an extremely small, spherical spore (about 5 µm) on a stalk one (E) or up to three times (F) reaching the spore diameter.

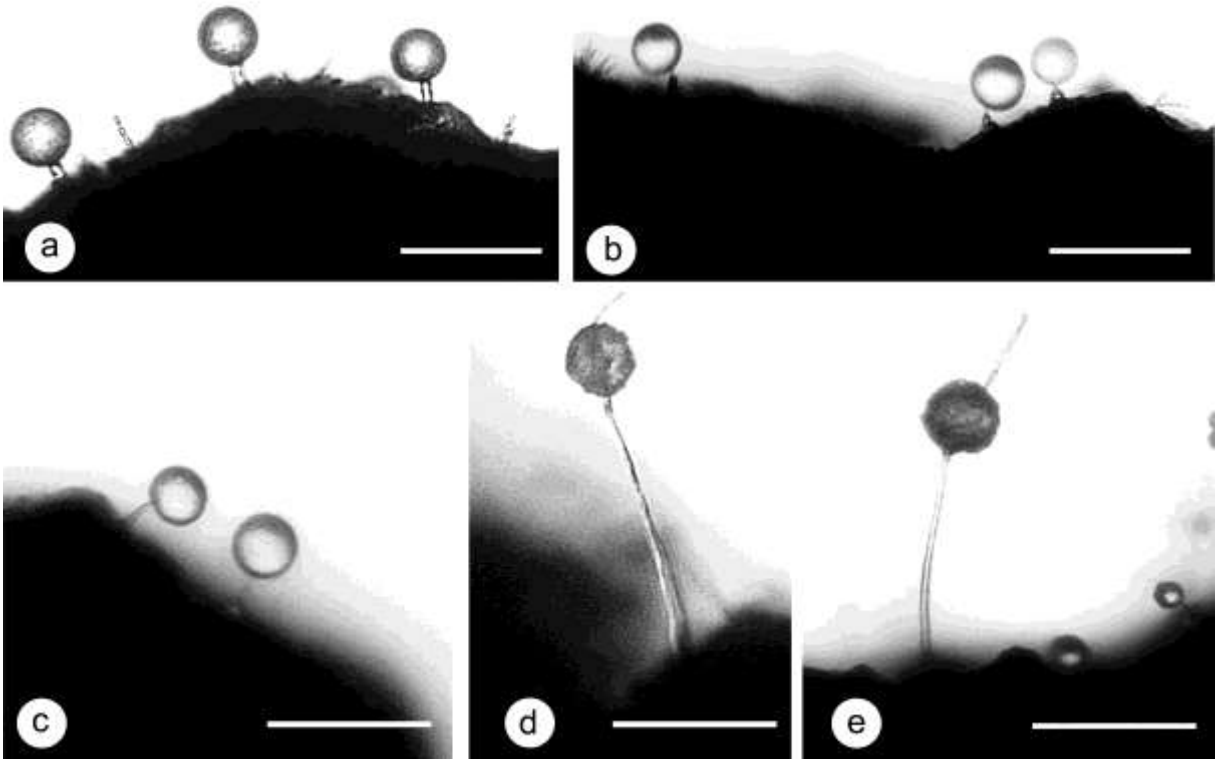

Fig. **2** – Unknown protostelid species from Oman; stacked images taken with a compound microscope. **a**. Protostelid species A, mc6254. **b**. Protostelid species B, mc 6267. **c**. Protostelid species C, mc6267. **d**, **e**. Protostelid species D, mc6244; spores sliding down in the stalk which collapses at its upper part. Scale bars = 50 µm.

Myxomycetes

Arcyria cinerea (Bull.) Pers. [C, 13] Mts: 10 Des: 1 Dho: 2+1 / b: 1 d: 4 l: 7 w: 1+1 / mc: 13, ag: 0 (30.5/- days), fc: 1, sc23459,…
Often the most abundant myxomycete in other surveys, in arid regions *A. cinerea* is comparatively rare.

Calomyxa metallica (Berk.) Nieuwl. [O, 3] Mts: 2 Dho: 1 / b: 3 / mc: 3, ag: 0 (18.5/- days), sc23300,…

Comatricha pulchella (C. Bab. & Berk.) Rostaf. [R, 1] Mts: 1 / l: 1 / mc: 1, ag: 0 (12.7/- days), sc23259.

Craterium rubronodum G. Lister [O, 3] Dho: 3 / l: 3 / mc: 3, ag: 0 (33.7/- days), sc23480, sc23500, … , Fig. 3a–d.
Sporocarps scattered, stalked, 0.2–0.7 mm total height. Sporotheca goblet- or saucer-shaped, 0.1–0.6 mm wide, smooth, pearl grey (pkWhite 9) or reddish grey (rGy 22), dark reddish-brown (d.rBr 44) at the base. Peridium somewhat cartilaginous, with uniform lime deposits on the outside, the lid well-defined, convex, concolorous with the cup, grey (l.Gy 264) to brownish (l.brGy 63) in transmitted light, smooth, with a rim turned upwards. Stalk dark red brown or black, shiny, slender, 0.1–0.4 mm tall. Hypothallus discoid. Capillitium of ovoid or irregularly rounded grey or slightly pinkish nodes connected by hyaline tubules, without pseudocolumella. Spore mass black (Black 267). Spores dark brown in TL, marked with scattered spines connected by ridges which form an incomplete reticulation, 10–12 µm diam.
Our material fits well this species, except for the color of lime nodes and absence of pseudocolumella. According to the original description the pinkish lime nodes and a large pseudocolumella are distinct characters of this species. However, the color of lime in Physarales is naturally variable and may change with the substrate (Aldrich 1982). In our specimens only several sporocarps possess slightly pinkish capillitium nodes, but the greater part of the examined sporocarps has grey nodes and lacks a pseudocolumella. Specimen sc23500 consists of only one but well developed sporangium together with numerous sporangia of *Physarum bivalve*.

Cribraria violacea Rex [O, 8] Mts: 1 Dho: 7 / b: 7 l: 1 / mc: 7, ag: 2 (21.9/19.0 days), sc23374,…

Diachea leucopodia (Bull.) Rostaf. [O, 3] Dho: 3 / l: 3 / mc: 3, ag: 0 (33.7/- days)

Dianema cf. ***harveyi*** Rex [O, 3] Mts: 3 / b: 3 / mc: 3, ag: 0 (22.8/- days), sc 23292,… , Fig. 3e–i.
Sporocarps sessile or small plasmodiocarps, ochraceous, pulvinate, 0.3–0.5 mm tall and 0.5–3 mm diam., olivaceous (d.gY 103) but lacking iridescence, perhaps due to development in moist chamber. Peridium membranous, thin and covered by granular deposits, smooth. Dehiscence irregular. Capillitial threads simple, filiform, stiff, sometimes forked at the points of connections, usually connected to the peridium, 1–1.5 µm in diam, evenly and densely fine warty. Spore mass yellowish olivaceous brown (l.Ol 106), spores globose to subglobose, (10.5)11.3–12.2(12.5) µm, covered with dense and fine warts.
Spore size and ornamentation of our specimens are typical for *D. harveyi*, but our specimens differ from the original description by the ornamentation of capillitial threads which are finely warted as in *D. depressum*.

Didymium anellus Morgan [A, 49] Mts: 34 Des: 13 Dho: 2 / b: 34 d: 4 l: 7 w: 4 / mc: 43, ag: 13 (18.3/14.1 days), sc21343, 23338, 23361,… , Fig. 4a–d.
As in other surveys of myxomycetes from arid areas, this species is common in the arid regions of Oman but was only once found in the Dhofar region. Remarkable for the species are the very pale (l.bGy 190 to l.OlGy), rather small spores ornamented with darker groups of more pronounced warts.

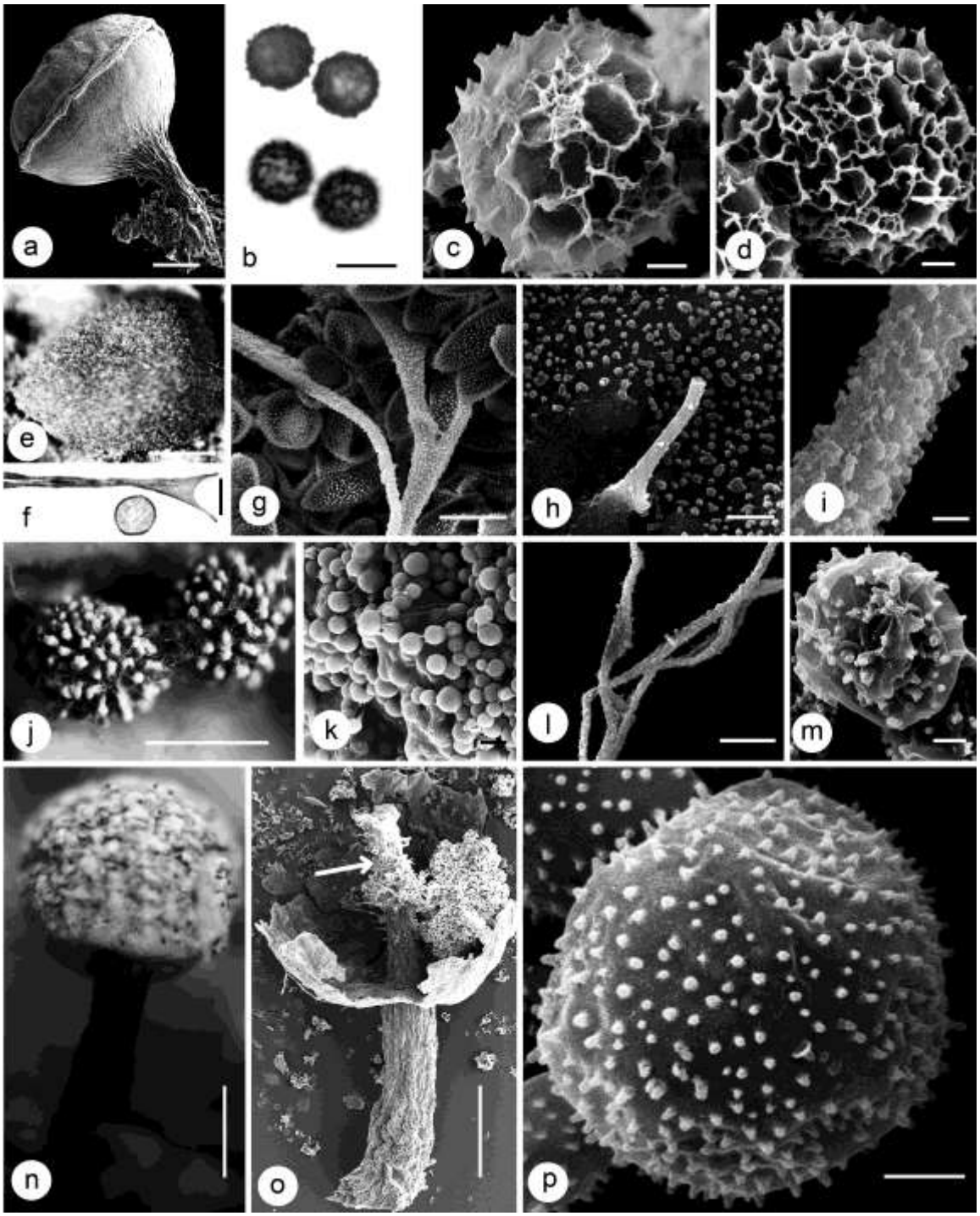

Fig. **3** – *Craterium rubronodum* (sc23480): **a**. SEM micrograph of a sporocarp showing the dehiscence line. Scale bar = 100 μm. **b**. Spores seen in the compound microscope (top and median view). Scale bar = 10 μm. **c, d**. Spores (SEM). Scale bar = 2 μm. *Dianema harvei* (sc23292): **e**. Sporocarp seen with the dissection microscope. Scale bar = 100 μm. **f**. Capillitium and spore; compound microscope. Scale bar = 10 μm. **g**. SEM micrograph of capillitial threads and spores. Scale bar = 10 μm. **h**. Inner surface of the peridium seen by SEM. Scale bar = 2 μm. **i**. Capillitial thread (SEM). Scale bar = 1 μm. *Physarina echinospora* (sc23507): **j**. Top view of two sporocarps showing baculeate limy outgrowths (Dissection microscope). Scale bar = 100 μm. **k**. Lime granules of peridial outgrowths (SEM). Scale bar = 2 μm. **l**. Capillitium (SEM). Scale bar = 5 μm. **m**. Spore (SEM). Scale bar = 2 μm. *Physarum crateriforme* (sc21364): **n**. Sporocarp (dissection microscope). Scale bar = 100 μm. **o**. Columella in an opened sporocarp (arrow, SEM). Scale bar = 100 μm. **p**. Spore (SEM). Scale bar = 1 μm.

Didymium difforme (Pers.) S.F. Gray [C, 14] Mts: 2 Des: 2 Dho: 10 / b: 1 d: 2 l: 9 w: 2 / mc: 13, ag: 1 (28.2/17.0 days), sc23381,… , Fig. 4e–g.
Beside *D. anellus* the most common of the sessile species of *Didymium*, easy to recognize by its spores: very dark brown (d.Ol 108 to d.OlBr 96) in transmitted light and ornamented with warts that are hard to recognize even with oil immersion, letting the outline of the spores to appear smooth. Only SEM micrographs reveal the ornamentation of dense and very shallow warts.

Didymium cf. ***annulisporum*** H.W. Keller & Schokn. [R, 1] Des: 1 / d: 1 / mc: 1, ag: 0, (40.0/- days), sc23504, Fig. 4m–n.
One but larger collection with sporocarps and short plasmodiocarps, superficially resembling *D. difforme* but outer calcareous layer not as smooth, more crumbled and of uneven thickness. Capillitium fairly abundant, stiff, with irregular swellings, these sometimes filled with lime, in transmitted light violet brown (pGy 233). Spores in mass almost black, in transmitted light very dark brown (d.Ol 108), (12)13–13.5(14) µm in diam., with unevenly distributed baculeate warts of about 0.5 µm height, these relatively dense but not evenly distributed (15–25 per spore diameter), in addition at least some spores with elevated ridges.
Spores are as dark as in *D. difforme*, but in contrast to the shallow warts of the latter species this specimen shows taller warts easy to recognize at the spore outline with a compound microscope, often accompanied by elevated ridges. The warts are arranged much denser than in *D. trachysporum* G. Lister, but are more prominent than in *D. difforme*. We tentatively assign our specimen to *D. annulisporum* although the spores are larger than given in the original description, here mentioned as (9)10(11) µm in diam. The ridges are not always easy to recognize in transmitted light (Keller & Schoknecht 1989).

Didymium spec. [R, 1] Des: 1 / b: 1 / mc: 1, ag: 1 (21.0/10.5 days), sc23392, Fig. 4h–k.
Sporangia or flattened sporocarps, sometimes with holes in it, solitary or scattered, sessile, yellowish–cream (yGy 93) or greyish white (White 263), subglobose if small or pulvinate on a wide base, 0.2–0.8 mm diam. Peridium membranous, covered by rather dense layer of small white or fawn lime crystals, these still visible, not forming a crust like in *D. difforme*. Columella absent. Capillitium scanty, dark violet brown (d.bGy 192), rather firm and stiff, sometimes remarkably undulate with occasional small swellings but free of lime. Spore mass very dark brown (d.OlBr 96), not black. Spores dark brown (d.OlBr 96 to OlGy 113), slightly angular or irregular in shape, in transmitted light conspicuous by darker fields surrounded by paler belts, densely and evenly covered with warts well visible in transmitted light, these up to 0.8 µm tall, (9.0–)9.5–10(–10.3) µm in size.
This taxon is characterized by the the dense but prominent warts and the pale and dark fields of the spores. The habit of sporocarps is similar to *D. inconspicuum* Nann.-Bremek. & D.W. Mitch. However, this species has larger spores (12–14 µm) that are more prominently verruculose and evenly colored without pale areas.

Didymium squamulosum (Alb. & Schwein.) Fr. [O, 5] Mts: 2 Dho: 3 / d: 2 l: 3 / mc: 4, ag: 1 (25.8/13.0 days)
Usually the most common species of *Didymium*, this species is rare in arid regions.

Echinostelium arboreum H.W. Keller & T.E. Brooks [O, 7] Mts: 4 Des: 1 Dho: 2 / b: 7 / mc: 4, ag: 3 (18.5/12.6 days)
Fairly common in arid zones of Eurasia.

Echinostelium bisporum (Olive & Stojan.) Whitney & Olive [A, 20] Mts: 14 Des: 3 Dho: 3 / b: 16 l: 3 w: 1 / mc: 0, ag: 20 (-/5.9 days)
This minute species with two spores on a short stalk was detected in agar cultures only, in surveys based in the moist chamber technique only it usually escapes detection.

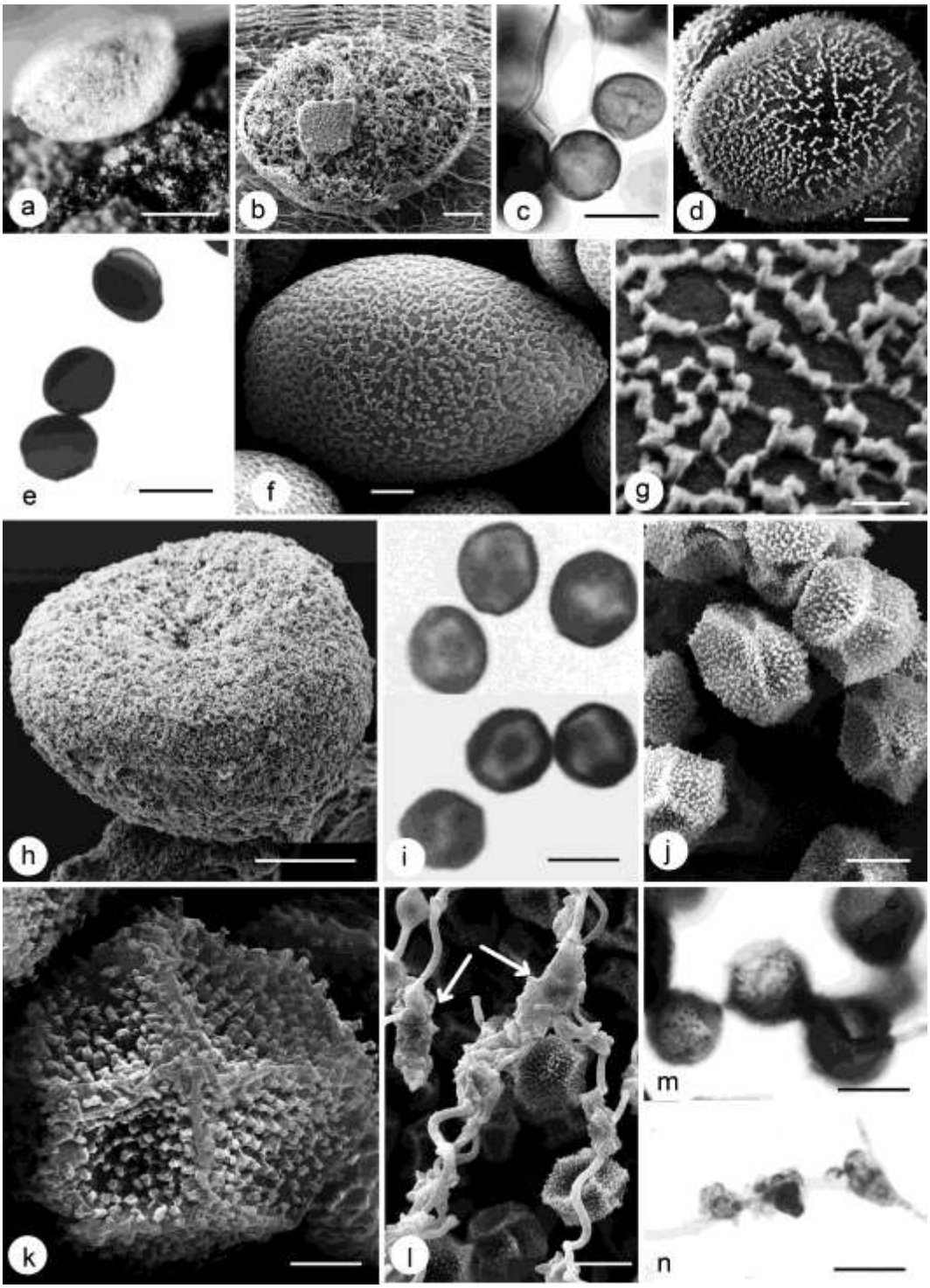

Fig. **4** – *Didymium anellus* (sc23397): **a**. Sporocarp seen under the dissection microscope. Scale bar = 100 μm. **b**. The same sporocarp opened, seen by SEM. Scale bar = 100 μm. **c**. Spores (compound microscope, top and median view). Scale bar = 10 μm. **d**. Spore (SEM). Scale bar = 2 μm. *Didymium difforme* (sc23381): **e**. Spores (compound microscope). Scale bar = 10 μm. **f**. Spore (SEM). Scale bar = 2 μm. **g**. Spore ornamentation consisting of shallow warts (SEM). Scale bar = 0.5 μm. *Didymium* spec. (sc23392): **h**. Sporocarp (SEM). Scale bar = 100 μm. **i**. Spores (compound microscope, top and median view). Scale bar = 10 μm. **j**. Spores (SEM). Scale bar = 5 μm. **k**. Spore ornamentation (SEM). Scale bar = 2 μm. **l**. Capillitium and spores seen with SEM (arrows indicate nodes with crystalline granules). Scale bar = 10 μm. *Didymium* cf. *annulisporum* (sc23504): **m**. Spores (compound microscope, top and median view). Scale bar = 10 μm. **c**. Capillitium, nodes filled with lime granula (compound microscope). Scale bar = 10 μm.

Echinostelium colliculosum Whitney & H.W. Keller [A, 65] Mts: 57 Des: 5 Dho: 3 / b: 56 l: 5 w: 4 / mc: 49, ag: 53 (8.2/7.6 days)
The most common species of *Echinostelium* in arid areas of Central Asia, in Oman especially common in the Hajar mountains. Fresh sporocarps may be slightly pink (p.yPk 31). For half (37 of 65) of all records the species was found in moist chamber as well as in the corresponding agar culture.

Echinostelium elachiston Alexop. [C, 11] Mts: 11 / b: 11 / mc: 11, ag: 1 (13.3/13.0 days)
A species described from and usually found in the Mediterranean region, the apparent restriction to the Hajar mountains fits well into this pattern.

Echinostelium lunatum Olive & Stoian. [R, 2] Mts: 2 / b: 2 / mc: 0, ag: 2 (-/6.5 days)
Another extremely small *Echinostelium* which can only be found in agar cultures.
Echinostelium minutum de Bary [O, 4] Mts: 4 / b: 3 l: 1 / mc: 4, ag: 0 (8.0/- days)
This largest of all *Echinostelium* species and the most common in temperate regions with moderate rainfalls, seems to be rare in arid zones.

Enerthenema papillatum (Pers.) Rostaf. [C, 9] Mts: 9 / b: 9 / mc: 9, ag: 0 (13.7/- days)
A few scattered sporocarps much smaller than usual, but with the typical disk-like apex of the columella.

Fuligo cinerea (Schwein.) Morgan [O, 3] Mts: 2 Des: 1 / b: 2 w: 1 / mc: 3, ag: 1 (27.3/13.0 days), sc 21354,…
Recorded scattered throughout arid regions of Eurasia.

Hemitrichia serpula (Scop.) Rostaf. [–, 1] Dho: 0+3/ w: 0+3 / fc: 3
Several weathered specimens from were seen in the Dhofar region on decaying wood, perhaps common during the rainy season.

Lamproderma arcyrionema Rostaf. [R, 1] Mts: 1 / l: 1 / mc: 1, ag: 0 (40.0/- days), sc 23452.
Found only once with four sporangia. However, the structure of capillitium, shape and size of columella and small (7–8 µm) minutely warted spores are typical for this species.

Licea biforis Morgan [C, 17] Mts: 15 Des: 2 / b: 15 l: 2 / mc: 15, ag: 6 (16.7/11.3 days)
Much more common than in the winter-cold deserts of Eurasia.

Licea denudescens H.W. Keller & T.E. Brooks [A, 34] Mts: 30 Des: 2 Dho: 2 / b: 34 / mc: 26, ag: 23 (12.7/13.3 days), sc21337,…
Sporocarps sessile, 0.2–0.4 mm diam., globose to hemispheric or rarely somewhat elongate, dull black (brBlack 65), or smooth and glossy brown (d.rBr 44) when the outer peridial layer has eroded. Peridium firm, consisting of two closely adhering layers, the inner layer membranous, thin, translucent, pale olivaceous brown (l.gy.Ol 109), prominently marked inside with outgrowths varying from papillae to somewhat irregular excrescences commonly forming an irregular, reticulate pattern, the outer layer black and opaque from refuse material, firm and brittle when dry, sometimes swelling when wet to a thick, generally hyaline, gelatinous layer. Dehiscence irregular. Spore mass glossy brown (d.rBr 44). Spores pale olivaceous brown (l.gy.Ol 109), globose or ovoid, smooth, with a sharply defined, colorless germination area, 8.5–11 µm diam.
For the minute species of *Licea*, agar cultures work as well as moist chamber cultures, since in many cases a species of *Licea* was found in moist chamber as well as in the corresponding agar culture (*L. biforis*: 4 of 17, *L. denudescens*: 17 of 34, *L. nannengae*: 3 of 9, *L. kleistobolus*: 3 of 23 records).

Licea nannengae Pando & Lado [C, 9] Mts: 9 / b: 9 / mc: 8, ag: 4 (15.5/14.3 days), sc23422, sc23466,…
Sporocarps scattered to gregarious, 0.05–0.2 mm diam., sessile, nearly globose on a somewhat narrowed to broad base, without platelets but with small iridescent ridges when dry. Peridium dark brown (d.Ol 108) to yellow-ochraceous (m.Ol 107), with deposits of granular refuse matter which,

when they are scanty, allow observation of the membranous inner layer, which is translucent, shiny and slightly iridescent, by TL, smooth, pale olive (l.OlGy 112). Dehiscence by fragmentation of the peridium, leaving a glossy cup. Spore mass dark brown (d.Ol 108). Spores globose, olivaceous brown (l.gy.Ol 109), thick walled with a thinner pale area, 9.5–13.5 µm diam. Our material fits well to the original description.

Licea kleistobolus G.W. Martin [A, 23] Mts: 23 / b: 23 / mc: 19, ag: 7 (12.2/12.3 days)

Licea tenera Jahn [O, 4] Mts: 4 / d: 4 / mc: 4, ag: 0 (40.0/- days), sc23441,…
One of the species of *Licea* similar to *Perichaena*, letting *Licea* appear as a non-natural genus; obligately coprophilous, regularly found in surveys in arid zones of Central Asia but never common. A description and taxonomic delimitation of the species is provided in Schnittler et al. (2012b).

Macbrideola cornea (G. Lister & Cran) Alexop. [C, 9] Mts: 9 / b: 9 / mc: 9, ag: 2 (22.1/12.0 days), sc23293,…
As the following species, fairly common in the Mediterranean and southern temperate zones.

Macbrideola oblonga Pando & Lado [A, 34] Mts: 32 Dho: 2 / b: 34 / mc: 34, ag: 13 (14.4/11.4 days), sc23292, sc23402, sc23415,…
A species described from the Mediterranean area and found regularly especially in arid zones of western Central Asia.

Macbrideola scintillans H.C. Gilbert [R, 1] Dho: 1 / b: 1 / mc: 1, ag: 0 (21.0/- days)
In contrast to the two other species of *Macbrideola* this species seems to have its main distribution in tropical dry forests, the records from Dhofar fit into this pattern.

Metatrichia vesparium (Batsch) Nann.-Bremek. [R, 1] Dho: 1+3 / b: 1+2 w:0+1 / mc: 1, ag: 0 (40.0/- days), fc: 3
Common in temperate and tropical zones, perhaps common during the rainy season in the Dhofar region.

Perichaena chrysosperma (Currey) Lister [O, 4] Mts: 3 Dho: 1 / b: 1 d: 2 l: 1 / mc: 3, ag: 1 (40.0/13.0 days)

Perichaena corticalis (Batsch) Rostaf. [R, 1] Dho: 1 / b: 1 / mc: 0, ag: 1 (-/21.0 days)

Perichaena depressa Libert [A, 23] Mts: 9 Des: 10 Dho: 4 / b: 4 d: 8 l: 9 w: 2 / mc: 23, ag: 0 (37.0/- days)
Very common in arid zones of Central Asia. This species is one of the few which were as common in the central desert as in other regions of Oman. The thick, shell-like peridium makes it resistant against desiccation during development.

Perichaena quadrata T. Macbr. [R, 1] Mts: 1 / d: 1 / mc: 1, ag: 0 (40.0/- days), sc23445.
We have only one specimen fitting the characters of *P. quadrata* as described in Keller & Eliasson (1992). Only molecular investigations can proof that *P. depressa* and *P. quadrata* are indeed separate species.

Perichaena liceoides Rostaf. [R, 1] Mts: 1 / d: 1 / mc: 1, ag: 0 (30.5/- days)
Another predominantly coprophilous species, rarely but regularly encountered in arid regions of Central Asia.

Perichaena vermicularis (Schwein.) Rostaf. [A, 44] Mts: 20 Des: 11 Dho: 13 / b: 27 d: 5 l: 9 w: 3 / mc: 41, ag: 4 (21.3/17.6 days)

Physarina echinospora K.S. Thind & Manocha [R, 1] Dho: 1 / d: 1 / mc: 1, ag: 0 (40.0/- days), sc23507, Fig. 3j–m.
Sporocarps short stipitate, gregarious or scattered, 0.5–l mm total height. Sporothecae pale creamy-grey (I.Gy 264), globose, 0.5–0.7 mm diam. Peridium thin, tough, brittle, calcareous, bearing

numerous blunt, cylindrical limy yellowish-white (p.YG 121) pegs , paler than other part of the peridium, 60–100 µm long and up to 70 µm diam. peridium reticulately ridged around the bases of the pegs. Dehiscence irregular. Stalk very short, about 5–10% of total height, stout, calcareous, concolorous with the pegs. Columella conspicuous, subglobose to columnar, calcareous, pale white (White 263) to light grey (I.Gy 264), extending to the middle of sporotheca. Capillitium abundant, non-calcareous, violet-brown (p.P 227), radiating from columella and tapered to the paler or hyaline tips, these sometimes anastomosing, often with membranous expansions at the points of union, readily detached. Spore mass black. Spores very dark (d.Gy 266 to pBlack 235), subglobose, slightly angular with a ridge surrounding each spore, letting it appear walnut-shaped in outline, and with numerous prominent and unevenly distributed spines, 11.2–14 µm diam., including the spines. Our material contains only four sporangia, but all features correspond well with the original description of this rare tropical to subtropical species.

Physarum bivalve Pers. [O, 3] Dho: 3+1 / l: 3+1 / mc: 3, ag: 0 (40.0/- days), fc: 1, 20229,…

Physarum cinereum (Batsch) Pers. [R, 1] Dho: 1 / l: 1 / mc: 1, ag: 0 (21.0/- days), 23387.

Physarum crateriforme Petch [R, 1] Dho: 1 / b: 1 / mc: 0, ag: 1 (13.0/- days), sc21364, Fig. 3n–p.
Sporocarps stipitate, 1–2 mm tall. Sporotheca globose to pear-shaped, clavate and crateriform after dehiscence of the peridium, 0.4–0.6 mm diam., greyish white (l.Gy 264) to pale brown (d.OlBr 96) at sporocarp base. Stalk black (Black 267) below but becoming pale from lime near the tip. Columella cylindrical, hollow, including dark deposits, reaching the apex of the sporotheca, concolorous with the stalk. Capillitium strongly calcareous, its nodes either massed about the columella or rod-like and ascending. Spores dull lilac (d.pGy 234), evenly spinulose, 10–13 µm diam.
Our material is very scanty and consists of only two but typical sporangia. The shape of sporotheca and columella is very distinctive. This species is another representative of the group of tropical to subtropical species of the Dhofar region.

Physarum decipiens M.A. Curtis [R, 2] Mts: 2 / b: 2 / mc: 2, ag: 1 (40.0/21.0 days), 21379, 23428.

Physarum didermoides (Pers.) Rostaf. [O, 4] Des: 3 Dho: 1+2 / d: 2 l: 1+2 w: 1 / mc: 4, ag: 0 (40.0/- days), fc: 2, 23478, 23481,…
Often occurring but not exclusively on herbivore dung and litter in arid regions. In the Neotropics often found on inflorescences of Zingiberales forbs (Schnittler & Stephenson 2002).

Physarum javanicum Racib. [O, 5] Mts: 1 Des: 1 Dho: 3+1 / b: 2 k: 0+1, l: 3 / mc: 5, ag: 0 (22.3/- days), fc: 1
Several collections of this predominantly tropical species from the Dhofar.

Physarum pseudonotabile Novozh., Schnittler et Okun [A, 107] Mts: 51 Des: 43 Dho: 13 / b: 43 d: 26 l: 19 w: 19 / mc: 99, ag: 13 (28.5/15.3 days)
In Central Asia this newly described species appears to be the most common myxomycete in moist chamber studies (Schnittler & Novozhilov 2000, Novozhilov & Schnittler 2008, Novozhilov et al. 2009, Schnittler 2012b). These specimens from arid zones are certainly not conspecific with the type of *P. notabile*, described by Macbride from upstate New York. Molecular investigations revealed that *P. notabile* s.str. is a species of the forest zone, preferring soft decaying wood (material from the US, Siberia and European part of Russia was investigated), whereas the material of arid deserts and steppes of Central Asia and Oman belongs to a second species (Novozhilov et al. 2013).

Physarum pusillum (Berk. & M.A. Curtis) G. Lister [R, 1] Dho: 1 / l: 1 / mc: 1, ag: 0 (30.5/- days), sc23490.
On grass litter from Dhofar, also fairly common in tropical zones.

Protophysarum phloiogenum M. Blackw. & Alexop. [R, 1] Des: 1 / w: 1 / mc: 1, ag: 1 (6.0/6.5 days), sc23265.

Surprisingly, only one record of this species was found, in both moist chamber and agar culture. Distribution data show that species to be highly restricted to arid zones around the world, the occurrence in the Central desert falls well into this pattern.

Stemonaria cf. ***clausifila*** Y. Yamam. & Nann.-Bremek. [R, 2] Mts: 2 / d: 1 l: 1 / mc: 2, ag: 0 (40.0/- days), sc23430, sc23454.
Sporocarps in dense groups, 2.4–3.0 mm tall. Sporotheca cylindrical with rounded ends, ca. 0.5–2 mm long, 0.3–0.6 mm diam., reddish-brown (m.rBr 43). Stalks reaching about one third of the total height, attenuate from a conical base, black (Black 267) to dark brown (d.rBr 44) and shining, hollow, opaque throughout by TL. Peridium early evanescent, not leaving a collar. Columella dissipating into the capillitium near the sporotheca apex. Capillitium brown (m.rBr 43 to l.rBr 42 towards the ends), rather lax, forming mostly 3–4 meshes across the radius, rather slender, closed and forming a few meshes (but not a net) on the surface, with some short, free ends, axils with membranous extensions. Spores pale vinaceous (L.rBr 42), 10–12 µm diam., densely spinulose. Our specimen fits best to *Stemonaria clausifila* although spore ornamentation differs slightly from the original description of this species (spores described as warted).

Stemonaria cf. ***fuscoides*** Nann.-Bremek. & Y. Yamam. [O, 3] Mts: 3 / b: 1 l: 2 / mc: 3, ag: 0 (40.0/- days), sc23450,...
Sporocarps in small groups, total height 4–5 mm. Sporotheca elongate to ovate, rounded at the base and apex, 2–3 mm tall and c. 0.5 mm diam., deep fuscous (d.rBr 44). Stalk black (Black 267), shining, 10–20% of the total height. Columella opaque, blackish, possessing small bulbous expansions at the end; not branching near the apex. Capillitium dark brown (d.rBr 44), forming a net with 2–3 meshes across the radius, with many pale brown (l.rBr 42) membranous expansions in the axils, the branches are mostly united just below the surface but do not form even an incomplete sub-surface net, very few free ends, all with 6–10 µm long outward-pointing branchlets near the surface. Spore mass deep fuscous (d.rBr 44) to dark brown (d.gy.rBr 47). Spores 9–10 µm diam., the ornamentation consists of rows of dark spinules, ca. 0.5 µm high, forming an incomplete reticulum with ca. 7 meshes across the diam.
The color of sporocarps, the spiny-reticulate spores, and the capillitium with an incomplete surface net with numerous branchlets near the surface, showing free ends and the bulbous extension on the end of the columella are typical for this species (Yamomoto 1999: 590). Since it is well known that Stemonitales often do not develop well in moist chamber cultures, we do not consider the determination of this and the previous species as certain.

Stemonitis fusca Roth [R, 2] Mts: 2 / b: 1 d: 1 / mc: 2, ag: 0 (40.0/- days), sc23455, sc23446.

Stemonitis splendens Rostaf. [–, 1] Dho: 0+1 / w: 0+1 / fc: 1, 20263.
Fairly common in tropical regions, the records from the subtropical Dhofar region fit into this pattern.

Trabrooksia applanata H.W. Keller [R, 1] Mts: 1 / b: 1 / mc: 0, ag: 1 (-/21.0 days), 23180.
A single collection of this species, described from the eastern United States, with all characters of the species. Remarkable are the stout, rigid capillitial threads connecting upper and lower peridium.

plasmodia not developing successfully [112] Mts: 67 Des: 12 Dho: 33 / b: 58 d: 10 l: 34 w: 10 / mc: 27, ag: 91
In numerous moist chambers and agar cultures we recorded phaneroplasmodia of Physarales. Not all developed successfully into fructifications, but a moist chamber where a plasmodium was recorded was counted as positive for myxomycetes.

Cultivation techniques: This is the first combined survey using agar and moist chamber cultures to detect MMLO in a given substrate sample. From the 299 cultures (one as a moist chamber, one agar culture) we obtained 591 and 875 records, respectively. Since species appeared twice in moist chamber and in the corresponding agar cultures, these figures summarize to only

1348 records. Table 1 shows the statistics for both types of cultures. Although not screened for protostelids, moist chamber cultures are more often positive for MMLO (76 vs. 64% for agar cultures), yield, if protostelids are not regarded, more records (591 vs. 389) in total as well as more taxa per culture (on average 1.76 vs. 1.16). However, moist chambers do not clearly outperform agar cultures for myxobacteria. They are less often positive for myxobacteria than agar cultures (18.4 vs. 22.1%) and have a lower yield (55 vs. 66 records, on average 0.17 vs. 0.27 taxa). In addition, a number of myxomycete taxa were recovered from agar cultures only (*Echinostelium bisporum*, *E. lunatum*, *Perichaena corticalis*, *Physarum crateriforme* and *Trabrooksia applanata*). Although represented by two species only, we obtained similar data for sorocarpic amoebae (5.4% positive moist chambers vs. 12.7% positive agar cultures; yield 17 vs. 39 records, on average 0.04 vs. 0.11 taxa).

From the 60 taxa recorded in this survey (neglecting the 25 protostelid taxa were only agar cultures have been screened), 22 were found in both culture types, although the degree of overlap was different for the groups of MMLO (Myxobacteria: 3 of 8 taxa recorded in both culture types, Sorocarpic amoebae: 1 of 2 taxa, Myxomycetes: 16 of 50 taxa). A considerable overlap in terms of records made for a substrate sample in both culture types exists only for a few common and small but not minute myxomycete species, e.g. *Didymium anellus* (8 of 49 records), *Echinostelium colliculosum* (37 of 65), *Licea denudescens* (17 of 34), and *Macbrideola oblonga* (13 of 34).

Regional species inventories: The three climatic regions of Oman differed sharply in their number of records: Mountains 943 (7.04 per substrate sample), Central Desert 156 (1.84 per sample), Dhofar 249 (3.11 per sample), and this pattern was consistent for all three larger groups of MMLO. The rarefaction analysis of the sample accumulation curves based on a minimum of 69 positive samples (without non-fruiting plasmodia) showed that the Dhofar is as diverse as the Mountains, although MMLO were found to be less abundant: Mountains 52.4 taxa, Central Desert 29.0, Dhofar 52.9. Fig. 5 presents the sample-based accumulation curves for the three regions. Figures for the species richness estimators Chao2 and Michaelis-Menten are as well comparable for Mountain and Dhofar regions but much lower for the Central Desert. Figures for Shannon diversity show a similar pattern with H' = 1.60 for the Mountain region, 1.21 for the Central desert and 1.55 for the Dhofar region.

Even based on presence-absence of taxa only, the three regions have different MMLO assemblages, values for the Soerensen coefficient are 0.40 for a comparison Mts. vs. Des., 0.48 Mts. vs. Dho. and 0.42 for Des. vs. Dho. A total of 21 taxa occurred in all three regions, 25 occurred solely in the Mountains, 4 exclusively in the Central Desert and 14 exclusively in the Dhofar region. These values do not consider the few field collections; all from the Dhofar region.

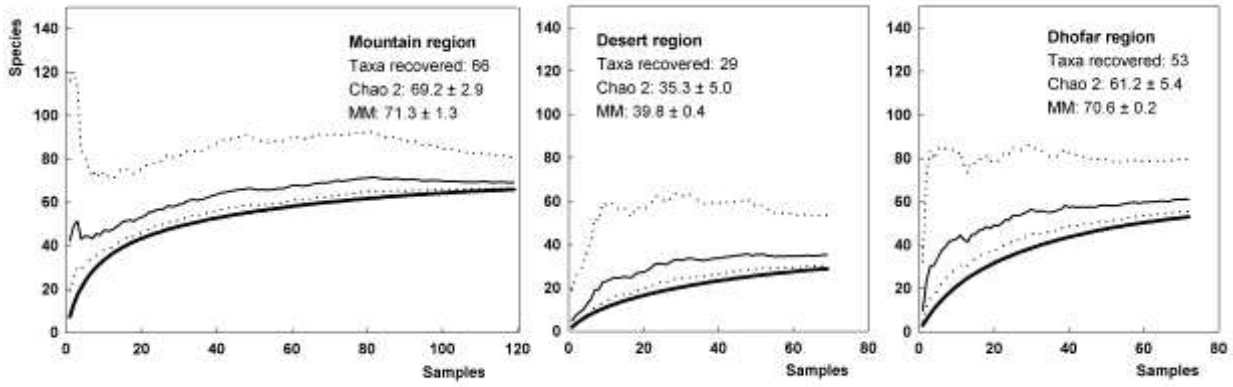

Fig. 5 – Species accumulation curves for the three climatic regions of Oman (thick solid lines). The thin line shows the Chao 2 estimator and its 95% confidence intervals (dotted lines). The figures "Chao2" in the graphs list its final mean value ± SD, "MM" the Michaelis-Menten estimator ± SD.

Table 1 Comparison of moist chambers (M) and agar cultures (A) for recovering MMLO diversity in the three climatic regions of Oman. Given are the percentage of positive cultures, total numbers of records, and the average number of taxa found in a culture. Moist chambers have not been examined for protostelids.

Positive cultures		**Total**		**Mts.**		**Des.**		**Dho.**	
mc's done	Culture	299		134		85		80	
positive (all MMLO)	M	226	75.6%	112	83.6%	65	76.5%	49	61.3%
	A	190	63.5%	99	73.9%	31	36.5%	60	75.0%
positive for Myxo-	M	55	18.4%	39	29.1%	11	12.9%	5	6.3%
bacteria	A	66	22.1%	34	25.4%	14	16.5%	18	22.5%
positive for Acrasids	M	16	5.4%	15	11.2%	1	1.2%	0	0.0%
	A	38	12.7%	32	23.9%	1	1.2%	5	6.3%
positive for Protostelids	M	n.d.		n.d.		n.d.		n.d.	
	A	134	44.8%	82	61.2%	12	14.1%	40	50.0%
positive for Myxo-	M	213	71.2%	104	77.6%	63	74.1%	46	57.5%
mycetes	A	128	42.8%	75	56.0%	17	20.0%	36	45.0%
Records									
all MMLO	M	591		404		107		80	
	A	875		637		63		175	
Myxobacteria	M	60	10.2%	44	10.9%	11	10.3%	5	6.3%
	A	83	9.5%	45	7.1%	17	27.0%	21	12.0%
Acrasids	M	17	2.9%	16	4.0%	1	0.9%	0	0.0%
	A	39	4.5%	33	5.2%	1	1.6%	5	2.9%
Protostelids	M	n.d.		n.d.		n.d.		n.d.	
	A	486	55.5%	369	57.9%	18	28.6%	99	56.6%
Myxomycetes	M	514	87.0%	344	85.1%	95	88.8%	75	93.8%
	A	267	30.5%	190	29.8%	27	42.9%	50	28.6%
Taxa per culture									
all MMLO	M	1.76		3.01		1.26		1.00	
	A	2.56		4.75		0.75		2.19	
Myxobacteria	M	0.17		0.33		0.13		0.06	
	A	0.27		0.34		0.20		0.26	
Acrasids	M	0.04		0.12		0.01		0.00	
	A	0.11		0.25		0.01		0.06	
Protostelids	M	n.d.		n.d.		n.d.		n.d.	
	A	1.40		2.75		0.21		1.24	
Myxomycetes	M	1.54		2.57		1.12		0.94	
	A	0.79		1.42		0.32		0.63	

Species preferences: Developmental times recorded in agar and in moist chamber cultures are usually similar for a given species, although large differences occur between species. Short developmental times have all protostelids (6.1±1.5 days, 25 taxa), *Acrasis rosea* (5.5 days), and some myxomycetes with minute fructifications, like the genera *Echinostelium* (9.4±3.9 days, 6 taxa), *Protophysarum phloiogenum* (6.4 days) and to a lesser extent *Macbrideola* (18.1±3.9 days, 3 taxa). All these species have minute (< 1 mm tall), stalked fructifications (usually with a stalk more than 2 times larger as the sporotheca diameter) with comparatively few spores (one for most protostelids, up to 200 in *Echinostelium*, only *Macbrideola oblonga* has more than 1000 spores). In contrast, the myxobacteria (14.5±8.6 days, 8 taxa), *Copromyxa* cf. *protea* (9.2 days) and the other myxomycetes (26.9±10.1 days, 41 taxa) develop much slower. These MMLO have usually sessile fructifications (30 of 49 taxa; in stalked forms the stalk is often not longer than the sporotheca diameter), and (except for the myxomycete genus *Licea*) much larger sporothecae with well over $5x10^5$ spores (Schnittler & Tesmer 2008). This assemblage occurs in other regions as well and inhabits all substrate types.

Table 2 Comparison of species assemblages for fast developing myxomycetes and myxomycete-like organisms (MMLO), and slow developing forms (see explanations in text). Shown are the statistics for the number of records and the number of species in the three different regions of Oman and for the four main substrate types cultured. Given are the proportion of the records/species of an assemblage on the total of records/species and records/species recovered on average per sample.

Regions / substrate types	Mts	Des	Dho	B	K	l	W	Total
Samples collected	134	85	80	104	84	79	32	299
Record Statistics								
Fast developing MMLO	504	28	110	492	12	126	12	642
Protostelids	369	18	99	351	12	117	6	486
Echinostelium, Macbrideola, Protophysarum	133	10	11	139	0	9	6	154
Acrasis rosea	2	0	0	2	0	0	0	2
Per cent of all records	53.4	17.9	44.0	58.1	10.7	41.2	14.3	47.6
Records per sample	3.76	0.33	1.38	4.73	0.14	1.59	0.38	2.15
Slow developing MMLO	439	128	140	355	100	180	72	707
Myxobacteria	86	23	25	48	24	35	27	134
Myxomycetes, other genera	311	103	110	285	75	121	43	524
Copromyxa protea	42	2	5	22	1	24	2	49
Per cent of all records	46.6	82.1	56.0	41.9	89.3	58.8	85.7	52.4
Records per sample	3.28	1.51	1.75	3.41	1.19	2.28	2.25	2.36
All MMLO	943	156	250	847	112	306	84	1350
Records per sample	7.04	1.84	3.13	8.14	1.33	3.87	2.63	4.52
Species Statistics								
Fast developing MMLO	30	11	25	29	4	18	5	36
Protostelids	21	7	20	19	4	15	3	25
Echinostelium, Macbrideola, Protophysarum	8	4	5	9	0	3	2	10
Acrasis rosea	1	0	0	1	0	0	0	1
Per cent of all species	44.5	37.9	47.2	47.5	15.4	38.3	27.8	42.4
Species per sample	0.22	0.13	0.31	0.28	0.05	0.23	0.16	0.12
Slow developing MMLO	36	18	28	32	22	29	13	49
Myxobacteria	7	4	5	6	5	7	4	8
Myxomycetes, other genera	28	13	22	25	16	24	8	40
Copromyxa protea	1	1	1	1	1	1	1	1
Per cent of all species	54.5	62.1	52.8	52.5	84.6	61.7	72.2	57.6
Species per sample	0.27	0.21	0.35	0.31	0.26	0.37	0.41	0.16
All MMLO	66	29	53	61	26	47	18	85
Species per sample	0.49	0.34	0.66	0.59	0.31	0.59	0.56	0.28

A comparison of these two assemblages reveals clear differences: Fast developing MMLO (7.7±4.0 days, 36 species) are more specialized than slow developing MMLO (25.0±11.1 days, 49 taxa). The former group includes mostly corticolous species (on average 4.74 taxa per sample) and represents 58% of all records on this substrate type (Tab. 2). Slow developing MMLO are as well most diverse on bark (3.41 taxa per sample), but occur regularly on other types of substrate. In a similar way, fast developing MMLO are more common and more diverse in the northern mountains, compared to all other regions (3.76 taxa per sample, 30 of 36 species found in this region). Slow developing MMLO are spread more evenly among the regions, although having also its highest diversity in the northern mountains. Interestingly, the central desert, being the most arid of the three regions, seems to be least suitable for fast developing MMLO, as for this region the differences in abundance (0.33 vs 1.52 records per sample) and diversity (11 of 36 *vs* 18 of 49 species) between the two assemblages are most pronounced.

These counts show that diversity and abundance of MMLO do not correspond directly with precipitation, as the mountains appear most suitable (7.04 taxa per sample, 66 taxa recorded, 95%

of all taxa expected according to the Chao2 estimator found, 200–350 mm annual precipitation). The Dhofar with a regular rainy season is equally diverse but MMLO occur more rarely in cultures, leading to a lower recovery rate (3.13 taxa per sample, 53 taxa recorded, 86% recovery rate, 600–900 mm precipitation if including monsoon fogs), although field collections during the rainy season should improve these figures. Least suitable is the desert region (1.84 taxa per sample, 29 taxa, 82% recovery rate, sporadic precipitation, usually less than 50 mm per year). Nevertheless, myxobacteria and fruit body-forming protists occurred at all desert sites investigated, even at places where nearly all vegetation was dead.

Among the most commonly sampled bark substrates (104 of 299 cultures were prepared with bark), the types b3 (peeling bark, 16 cultures) and b4 (fissured bark 83 cultures) are much overrepresented, which reflects the bark types of the natural vegetation: most shrubs and trees displayed peeling or fissured bark. Productivity of both moist chamber cultures and agar cultures was clearly higher for the bark type b4, when seen as records per culture: 1.8 / 4.3 for moist chamber / agar from peeling bark *vs* 3.7 / 6.4 for fissured bark.

Discussion

The survey presented here is the first systematic survey for Myxomycetes and similar organisms for the Arab Peninsula, and except for a report on dictyostelids (Hagiwara 1991) this is to our knowledge the first report about this group of organisms for the Sultanate of Oman. Since the field survey was carried out during the dry season, it almost exclusively relied on substrate collections, analyzed by two complementary approaches, moist chambers and agar cultures. The first technique is the classical approach for the detection of especially of minute myxomycetes, invented by Gilbert & Martin (1933) and extensively used for many surveys, e.g. by Härkönen (1977), Härkönen & Ukkola (2000). This approach works very well in arid regions (e.g., Novozhilov & Schnittler 2008) but the percentage of positive moist chambers as well as the number of taxa recovered decreases sharply in areas with high annual precipitation, like tropical mountain forests (Schnittler & Stephenson 2000). Another limitation is the size of a species: although occasionally large colonies of protostelids can be seen in moist chamber cultures, fructifications of this size can usually not be detected easily with a dissecting microscope. Even if the magnification of an excellent instrument would allow this, the field of view becomes very small and screening of the whole surface of a Petri Dish (about 60 cm^2 for standard dishes of 9 cm diam.) would be very time-consuming. Therefore, the smallest myxomycetes like *Echinostelium bisporum* (two-spored fructifications of 18–25 µm height) or *E. lunatum* (4–8 spores) usually escape detection by this method: both species were not found in a number of surveys in arid Central Asia carried out with the moist chamber culture technique (Caspian Lowlands: Novozhilov et al. 2006; Mongolia: Novozhilov & Schnittler 2008; Altai region: Novozhilov et al. 2009; Western China: Schnittler et al. 2012b). On the other hand, myxomycetes usually forming large colonies appear rarely in moist cambers: in this survey *Metatricha vesparium* was found once in moist chambers, but three times in 12 weathered field collections from the Dhofar region; *Hemitrichia serpula* was found three times in the field as well but appeared never in moist chambers. A standard Petri Dish, containing usually between 1 and 10 g dry substrate, seems not to provide enough resources for such species to complete their life cycle.

In arid regions, bark of living trees, litter and herbivore dung are most important substrates for such cultures, yielding in this survey 62, 50 and 25 taxa, respectively. Especially herbivore dung harbors a whole group of myxomycetes (Eliasson & Lundqvist 1979, Eliasson & Keller 1999, Schnittler 2001), in this survey represented by five taxa exclusively found on this substrate type.

Agar cultures were found to be an efficient method to detect protostelids (Spiegel et al. 2004, 2007); the relatively weak, resource-poor agar used for this approach keeps competing fungal growth at a minimum. Noteworthy is the high number of protostelid taxa detected in this study from an arid region: the two other studies reporting high protostelid diversity come from the humid tropics (Hawaii, 33 taxa, Spiegel et al. 2007; Congo, 23 taxa, de Haan et al. 2014). As demonstrated in this survey, this approach is also suitable to detect the smaller myxomycetes (except for the two

species of *Echinostelium* mentioned above, four rare myxomycetes and *Acrasis* cf. *rosea* were detected exclusively in agar cultures). Although the percentage of positive cultures was lower than for moist chambers, the method was extremely effective for detecting protostelids. The two species of *Protosporangium*, so far reported to be rare (Spiegel et al. 2007), were found to be common and specialized on bark of living trees. Agar cultures, if additionally checked with a dissecting microscope, work also well for myxobacteria, the only group of MMLO recovered equally well in moist chambers and agar cultures (77 and 120 records, respectively, six taxa found with both approaches). However, myxomycetes with larger fructifications and/or colonies are usually absent in these cultures, or develop with a few sporocarps only, as it was the case for *Physarum crateriforme*. Substrate pieces to be used in such cultures have best to be small (best 1 x 2–4 mm) but comparatively tall (1–2 mm), since only at the outline MMLO can be detected with the use of a compound microscope. Arranging a fixed number of such pieces in a line (streak) helps not to loose orientation if one checks cultures with a compound microscope, following the outlines of substratum pieces. In this survey, we used 4–6 substratum pieces in 4 streaks, giving a total of 120–200 mm outline to scan for the presence of MMLO.

Interestingly, dictyostelids have not been detected at all in this survey, although this is as well a common group of MMLO. Two reasons are conceivable. First, the usually used culture technique to recover dictyostelids involves soil dilutions to be spread on agar, since these MMLO occur primarily in the soil-litter interface (Bonner 1959). Second, dictyostelids seem to be much less adapted to arid conditions than all other MMLO, as their diversity hot spots are in tropical moist forests (Swanson et al. 1999).

Summarizing, the ideal (but time-consuming) approach for a all-taxon inventory of MMLO would consist of soil isolation cultures for dictyostelids, agar cultures with discrete substratum pieces for all minute MMLO, moist chambers with larger substrate pieces and a field survey component. Unfortunately, a single method equally suitable to detect all MMLO does not exist.

Comparing the three regions of the country, the large differences in climate and subsequently vegetation seem to be well reflected by MMLO, although in difference to vascular plants propagules for effective long-distance dispersal are formed. For myxomycetes, effective long-distance dispersal via airborne spores was demonstrated by Kamono et al. (2009). By far the highest number of records was recovered from the northern Mountains (on average seven taxa per substrate sample, Tab. 1), and this region was also richest in species (66 taxa). This was especially caused by the abundance and diversity of protostelids (especially on tree bark), accounting with 21 taxa for 39% of all records. For this region, no field collections could be made in spite of repeated attempts especially in the juniper woodlands of the summit region. The Chao 2 estimator for the species saturation curve seems to converge (Fig. 5), indicating that most of the diversity was recovered (95% of all taxa to be expected). With common species like *Macbridola cornea* and several of the genus *Licea*, the species assemblage bears some resemblance to that of Mediterranean areas, which is paralleled by some vascular plants (e.g., *Olea europaea* reaches its southernmost distribution in the Hajar Mts.).

As to expect, the Central Desert with only sporadic rainfalls and scattered Fabaceae trees in depressions was poorest in records (157) as well as species (29), and there were nearly no species exclusively found in that region, except for a form of *Nannocystis* spec. (Myxobacteria), and *Protophysarum phloiogenum*, a myxomycete that seems to be restricted to arid regions (Castillo et al. 1998). Remarkably, the only of the common myxomycete species that was most frequent in the Central Desert was *Physarum pseudonotabile*, found in 38% (Mts.), 51 (Des.) and 16 (Dho.) of all substrate samples. This species seems to represent a rather variable, not yet described taxon present in arid zones all over Eurasia. The high frequency especially in the central desert reflects its preference for arid regions. For the Central desert, the Chao 2 estimator converges as well, 82% of all taxa to be expected according to this estimator have been recorded. As to expect for extreme conditions (Odum 1971), the MMLO assemblage of this region is comparatively poor but has a higher proportion of dominant species, which is reflected by the higher figure for Simpson's D (0.10 in comparison to the two other regions, Mountains 0.03, Dhofar 0.04).

In terms of species richness, the Dhofar region is comparable with the Mountain region (53 taxa plus two myxomycetes from field collections), but the average frequency of MMLO is remarkably lower (on average three taxa per substrate sample). In other words, many more species appear to be rare, which is reflected by the Chao 2 estimator (Fig. 5) indicating that only 86% of all species to be expected have been recovered. However, as for vascular plants (here with a high proportion of endemic species), this region differs as well for MMLO in two aspects: First, the MMLO assemblage is most distinctive (14 species exclusively, two more predominantly appearing in this region). For myxomycetes, these species have often with a main distribution in tropical regions, like *Craterium rubronodum*, *Diachea leucopodia*, *Macbrideola scintillans* (exclusively Dhofar), or *Cribraria violacea* (seven of the eight records in this region). Second, the weathered field collections suggested that a whole assemblage of myxomycetes with larger fructifications appears during the rainy season, which could be adequately recovered by culture techniques. Adequate recovery of myxomycete diversity seems to depend from field collections, which can effectively only be made during the rainy season. This does not apply for Protostelids: only one rare taxon was exclusively found in this region; the diversity is comparable to that of the Mts. (21 vs. 20 taxa), and 16 of the 25 taxa have been found in both regions. The two corticolous species of *Protosporangium* are an exception, being much underrepresented in the Dhofar: 42 vs. 3 records for *P. articulatum*, 35 vs. 2 records for *P. conicum*.

Comparing the two different strategy types found (fast and slow developing MMLO), species of the first assemblage display a high preference for the northern mountains, and, to a lesser extent, for the Dhofar, but are much less common in the central desert (Tab. 2). The latter region has sporadic rainfalls only, thus our expectation was that members of the first strategy type are most suited to develop quickly after a single rainfall event. Instead, slow developing MMLO are comparatively more common in the desert. The best explanation is that the larger, much more robust plasmodia of slow developing MMLO are able to survive desiccation by reverting into sclerotia and can make use of compact substrata like fleshy plant parts, or dung. Thick, rigid peridia (as in most Physarales, or the genus *Perichaena*) allow sporocarps to develop as well in rather dry air. In contrast, the fast developing MMLO have usually none (many protostelids) or only protoplasmodia (*Echinostelium*), and the developing sporocarps have none (protostelids) or an evanescent (*Echinostelium*, *Macbrideola*) peridium and can only develop in rather humid air. The high preference for bark points towards dewfall as an important precondition for sporocarp development. During the survey taking place in the dry season we observed dew every night in the mountains, but never in the two other regions. In the Dhofar, mist is common only in the monsoon season. This would explain the preference of fast developing MMLO for the northern mountains, although the annual precipitation in the Dhofar is comparable or higher, if the fog equivalent is considered as well.

Summarizing, we can conclude that MMLO can be detected in a joint approach, although at least three culturing techniques, namely agar cultures with discrete substrate pieces, moist chambers and (for dictyostelids) agar cultures with soil suspension have to be used together with field collecting. There is considerable overlap between the spectrum of species detectable in agar cultures and in moist chamber, but no method alone can detect the whole diversity of myxomycetes as the most species-rich group of this ecological guild. With decreasing size of the fructifications, the optimum species yield moves from field surveys over moist chambers to agar cultures. The smallest MMLO have not their optimum in deserts but in arid regions with regular mist or dew formation, as they are often specialized on tree and shrub bark. Steppes and semi-deserts harbor mostly minute MMLO with short development times (Schnittler 2001), thus culture techniques should be given more attention for these ecosystems. This is reflected by the high number of both taxa per culture and proportion of positive cultures in arid regions. Even in hyperarid regions with only sporadic rainfalls, as the Central Desert of Oman, a number of MMLO seems to be present with permanent populations.

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