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Isolation of zoosporogenous actinomycetes from desert soils

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We have undertaken a study to estimate the species diversity of zoosporogenous actinomycetes that can be isolated from an arid environment. The study site encompassed an area of approximately 22 000 square kilometers of the Mojave Desert along the California-Nevada border. A series of 29 soil samples was collected along two intersecting transects of approximately 190 and 240 km which traversed a number of distinct ecosystems. A_0 horizon soils were collected from the rhizosphere of the predominant vegetation at each sampling site and screened for the target genera using selective isolation techniques: chemoattraction (xylose and γ-collidine) and baiting with hair. Following incubation of primary isolation plates for 28 days at 28°C, all colonies that exhibited filamentous growth, presence of sporangia and/or motile spores upon direct microscopic observation (450 and 1000 ×) were further characterized by fatty acid analysis (FAME). Most of the isolates fell into three broad clusters that roughly correlated with presumptive genus assignments. Individual isolates could be assigned to 226 FAME biotypes based on chromatographic similarity (≥85%). The dominant species (514/826 isolates) belong to a previously undescribed taxon that morphologically resembles *Geodermatophilus* but possesses unique FAME profiles that include at least three novel lipids. The remainder of the isolates were species of *Actinoplanes*, indeterminate species or vagrant isolates of *Streptomyces*.

Keywords: *Actinoplanes*; actinomycetes; desert; ecology; FAME; fatty-acid analysis; *Geodermatophilus*; zoospores

Introduction

Among the free living saprobic bacteria, actinomycetes may have the widest extent of survival strategies, thereby allowing them to persist in soils under extreme conditions. These strategies range from the formation of desiccation-resistant resting cells (eg *Arthrobacter, Rhodococcus, Microbacterium, Corynebacterium*) to the production of simple or elaborate structures that bear either non-motile (eg *Micromonospora, Actinomadura, Streptomyces, Streptosporangium*) or motile spores (eg *Planomonospora, Dactylosporangium, Actinoplanes, Spirillospora, Actinosynema, Geodermatophilus*) that may be chemotactic, aerotactic, or both.

Actinomycetes produce a wide range of secondary metabolites with pharmacological activity and the major focus on this group has been on the recovery of 'novel' species for industrial screening [8]. As a result, most of our knowledge of the ecology of these organisms has been gained indirectly rather than through systematic surveys [21,29]. Despite their economic importance, relatively little is known about the distribution of these organisms in nature, their relative abundance, the factors influencing their ability to compete successfully for resources within a niche or the role that each genus/group plays in the carbon cycle.

The production of motile spores is an interesting evolutionary adaptation. Initially, one would infer that an organism producing such propagules would be found in or surrounding an aquatic or marine environment. *Actinoplanes* spp can be found in littoral zones, along the edges of streams and lakes, and from other areas that undergo periodic wetting and drying, but members of this genus are rarely recovered from areas that are constantly submerged [2,6,18,25,27,28,30]. Zoosporogenous actinomycetes also occur in arid soils and *Geodermatophilus* spp may be present in high numbers [1,7,15,27].

Over time, several selective isolation methods have been developed that increase the number of zoosporogenous actinomycetes that can be recovered from various environmental materials. These include baiting with pollen, hair, or *Paspalum* grass and the use of chemoattractants toward which the zoospores will swim [4,5,11–13,22,23,26]. Distinguishing among strains however, has been difficult. The taxonomy of most of these groups is poorly developed above the genus level and heavily weighted for morphological features that overlap significantly and may not always be expressed in culture [9,10,27,28]. Gas chromatographic analysis of whole cell fatty acid methyl esters (FAME) can be employed to characterize rapidly and reproducibly actinomycetes at the genus level and above [3,14,20,24]. We have employed this technique extensively to differentiate among wild-type isolates. As a result, it is now possible to undertake a survey of actinomycetes isolated from a particular niche. We have undertaken such a study to estimate the species diversity of zoosporogenous actinomycetes that can be isolated from an arid environment. The study site encompassed an area of approximately 22 800 square kilometers of the Mojave Desert along the California-Nevada border and includes some of the hottest, driest and harshest environments in North America [16].

Materials and methods

Collection and processing of soil samples

Soil samples were collected over a 3-day period (May 20–22, 1994) along two intersecting transects of approximately

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190 and 240 km along the eastern and western slopes of the Panamint mountains. Samples (10–15 g) were taken from the rhizosphere of the visually predominant vegetation in each distinct ecosystem encountered (Table 1). Prior to isolation, soils were air-dried at 30–37°C for 7–14 days then gently pulverized with a sterile mortar and pestle.

Cultivation and maintenance of isolates

Working stocks of isolates were maintained on slants of SNY agar (10 g sucrose, 0.5 g yeast extract, 1.0 g $NaNO_3$, 0.1 g $MgSO_4 \cdot 7H_2O$, 15 g agar, 2 ml 1 M KPO_4 buffer pH 7.0, and 2.5 ml trace salts solution per liter). Phosphate buffer and trace salts were added aseptically after autoclaving them. Trace salts solution contained 4 g $CaCl_2 \cdot 2H_2O$, 2 g $MnSO_4 \cdot H_20$, 1 g $FeSO_4 \cdot 7H_20$, 0.05 g $ZnSO_4 \cdot 7H_20$ in one liter of 0.1 N HCl.

Isolation of actinoplanetes

Two isolation strategies were employed: baiting and chemotaxis. Chemotactic isolations were carried out using a modification of the method of Palleroni [11,22,23; JC Ensign, personal communication]. Briefly, 0.5 g of pulverized soil was placed into a sterile scintillation vial, flooded with 5 ml of sterile distilled water, and incubated for 30 min at 37°C. Solutions of two chemoattractants, γ-collidine and xylose, were drawn into sterile 5-μl PCR capillaries and the open tips of the capillaries were then immersed just below the surface of the water above the soil samples. Samples were then incubated for an additional 30 min at 37°C. Following incubation, the capillaries were gently withdrawn and the outside surface washed in a small stream of sterile water. The contents of the PCR capillary were then expelled into 2 ml of sterile distilled water and aliquots were directly plated onto SNY supplemented with Benomyl (7.5 ppm) (Rockland Chemical Co, West Culdwell, NJ, USA) to suppress fungal growth. Plates were incubated for 21–28 days at 28°C. Following incubation, all colonies exhibiting mycelial growth when observed directly at 450 × were transferred to appropriate media for morphological characterization and FAME analysis.

Keratinophilic actinoplanetes were recovered by baiting with hair using a modification of the method of Karling [13]. Air-dried soils (2 g) were placed into sterile glass Petri dishes and flooded with 25 ml sterile tap water. Baits (sterilized dog hairs approximately one half inch in length) were floated on the surface, after which the dishes were incubated in the dark for 28 days at 28°C. Following incubation, hairs were inspected microscopically and those exhibiting sporangia were transferred to sterile Whatman No. 2 filters and washed with sterile distilled water under vacuum on a mini-sieve fitted with a polypropylene support (105-micrometer pore size). The washed hairs/filters were air-dried for 7 days at ambient temperature, placed into sterile 60-mm Petri dishes, flooded with 10 ml sterile tap water and incubated for 60 min with occasional gentle agitation. At that time, the dissociated hairs and tap water were transferred to sterile test tubes, vortexed, diluted (10^{-1}–10^{-3}) and plated on Czapek's, YCZ and soil extract agar supplemented with novobiocin (100 μg ml^{-1}), nystatin (100 μg ml^{-1}) and actidione (200 μg ml^{-1}). The latter medium was also supplemented with small fragments of sterile hair. Following 21–28 days incubation at 28°C in the dark, all col-

Table 1 Soil samples used

Sample	No isolates	Environment	Predominant species
Soil 02	91	open desert	desert holly
Soil 03	3	open desert	bur sage
Soil 04	62	open desert	desert holly
Soil 05	2	open desert	unidentified
Soil 06	4	fresh water spring	palm litter
Soil 07	0	fresh water spring	grass
Soil 08	0	salt flat	salt grass
Soil 09	2	salt creek	pickleweed
Soil 10	0	salt cree, high water mark	pickleweed
Soil 11	0	salt creek, above high water mark	pickleweed
Soil 12	7	open desert	arrowweed
Soil 14	38	sand dunes	salt brush
Soil 16	17	sand dunes	honey mesquite
Soil 21	0	salt flat	pickleweed
Soil 23	6	salt water spring	pickleweed
Soil 25	8	open desert	creosote bush
Soil 27	0	salt spring	junca
Soil 28	39	open desert	creosote bush
Soil 29	115	open desert	purple mat
Soil 30	2	open desert	desert sage
Soil 31	1	open desert	unidentified
Soil 35	36	fresh water spring	junca
Soil 36	18	open desert	creosote bush
Soil 37	3	open desert	bur sage
Soil 41	38	open desert	honey mesquite
Soil 42	153	open desert	base of decaying cactus
Soil 44	74	open desert	brittlebush
Soil 45	33	open desert	unidentified senescent shrub
Soil 51	74	open desert	Joshua tree

onies exhibiting sporangia when observed directly at 450× were transferred to appropriate media for morphological characterization and FAME analysis.

Analysis of whole cell fatty acids by gas-liquid chromatography

Cultures were grown as confluent patches on 60-mm plates of YCZ/3 (one third strength Difco Czapek's DOX broth supplemented with 0.5 g Difco yeast extract and 20 g BBL agar) at 28°C for 10 days. Vegetative growth (approximately 60–80 μg) was gently scraped from the surface with sterile, stainless steel spatulas and placed into Teflon-capped test tubes. Fatty acid methyl esters (FAMEs) were prepared and extracted by the procedure of Miller and Berger [19]. Analysis of the FAMEs was accomplished by capillary gas chromatography using a Hewlett-Packard Model 5890 gas chromatograph/MIDI system (Microbial ID, Newark, DE, USA) equipped with a 5% phenylmethyl silicone column (0.2 mm × 25 m). Chromatography conditions were as recommended by the manufacturer. Peak areas were calculated using a Hewlett-Packard Model 3396 series II integrator. Individual FAMEs were identified on the basis of retention time which is a function of equivalent chain length, using the Microbial Identification System software. Quantities of each fatty acid are expressed as percentages of the total named FAME peak area.

Data analysis

Fatty acid data were exported from the MIDI environment into S-Plus (Ver 3.2 for Windows, Statistical Sciences, Seattle, WA, USA) in ASCII text format. FAME data were initially examined using principal component analysis to determine the relative degree of separation and uncover outliers. Iterative hierarchical cluster analysis was performed by first calculating absolute distance among the strains followed by clustering using the average-linkage algorithm. Bousfield's observational similarity coefficient (S_{mO}) was calculated from the matrix of absolute distances and used to establish probable boundaries for species ($S_{mO} \geqslant 85\%$) and strain level ($S_{mO} \geqslant 90\%$) relationships [3; Garrity, unpublished]. Upon each round of clustering, the underlying similarity matrix was sorted so that the leading and trailing nearest neighbors appeared on the first subdiagonal. Adjacent strains that showed $S_{mO} \geqslant 90\%$ were averaged and represented as centroid FAME profiles in subsequent rounds of clustering. Clustering stopped when no further strains were found to link together at this level. The clustered (represented as centroids) and unclustered strains were then compared to FAME profiles of 606 known and type strains of 43 genera of actinomycetes to determine probable identity. Those strains that exhibited $S_{mO} \geqslant 85\%$ to a type or reference strain were considered to be members of that species. Those which failed to join with a known species were identified as members of previously undefined species. The resulting identifications were then used to estimate species diversity. Since baiting and cheomattraction are highly selective methods of isolation, the Brillouin diversity index (HB) and measure of equitability (E) were employed, as randomness of sampling is not assumed [17].

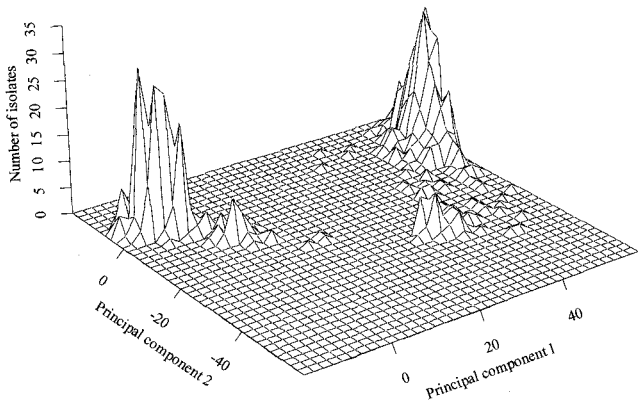

Figure 1 Density plot of zoosporogenous actinomycetes recovered from the Mojave Desert. FAME profiles for 826 isolates were examined using principal component analysis (PCA). The first two principal components accounted for 87.9% of the cumulative variance. The PCA scores were partitioned into a 38 × 38 grid space and the strains falling into each cell in the grid were tallied. *Actinoplanes* and the bulk of indeterminate species appear in the large peak on the left. *Streptomyces* spp appear in the smaller peak on the left, with some overlap with the *Actinoplanes*. *Geodermatophilus*-like spp appear in the large peaks on the right.

Results and discussion

The goal of this study was to determine the relative abundance and diversity of motile spored actinomycetes present in an extreme, arid environment. As these organisms are thought to be relatively rare, highly selective isolation techniques were employed. Six soils failed to yield any members of target genera. From the remaining 23 soils we recovered 826 isolates. The number of isolates per soil varied widely ranging from 1–153, with a median of 31 (Table 1).

The majority of isolates were expected to be *Actinoplanes* and *Pilimelia* spp along with a small number of vagrant non-motile actinomycetes. However, direct microscopic examination of colonies revealed that a large number of the isolates were strains of a zoosporogenous actinomycete with multilocular-sporangia resembling *Geodermatophilus obscurus* (514/826). The remaining isolates were initially assigned to three other generic groups based

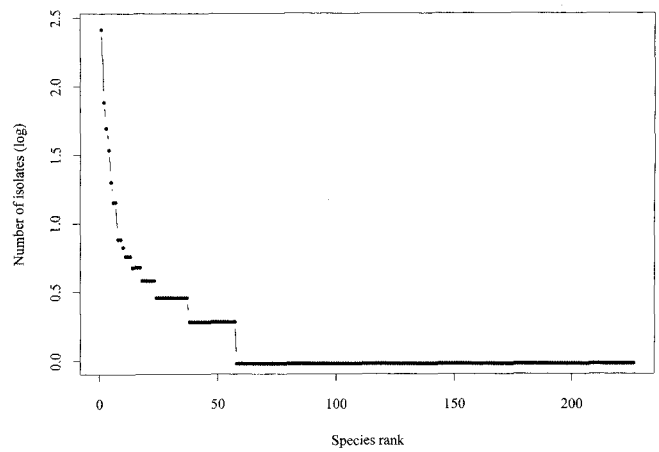

Figure 2 Rank abundance plot for zoosporogenous actinomycetes from the Mojave Desert. Following FAME analysis, strains were assigned to species based on $S_{mO} \geqslant 85\%$. The number of isolates were tallied and plotted in rank order of species occurrence.

on micromorphology: *Actinoplanes/Pilimelia* (167 isolates), indeterminate (92) and *Streptomyces* (53).

FAME analysis was performed on each isolate to gain further insight into probable identity. The first step in exploring the chromatographic data was to perform a principal component analysis on the entire data matrix. This unsupervised technique uncovers the linear combination of variables (fatty acids) that explain the maximum variance within the data. In the case of these data, the first two principal components accounted for 87.9% of the cumulative variance. This finding indicates that a PCA-density plot would fairly represent the 'biotopology' of the strains in the given taxonomic space (Figure 1). Two major peaks appear in these plots. The *Actinoplanes* isolates fall into the left peak and the *Geodermatophilus*-like isolates are found in the larger peak on the right. The indeterminate species mapped mainly into the region beneath the *Actinoplanes* peak with a small number of isolates also appearing in the region of the *Geodermatophilus*-like isolates. *The Streptomyces* isolates also overlap slightly with the *Actinoplanes* isolates, however most project further to foreground, in the separate minor peak.

To explore the relationships among these strains further, iterative hierarchical clustering was performed. Using this approach, the 826 strains could be assigned to 226 distinct FAME biotypes. The reduced FAME data matrix was then merged with a data set containing FAME profiles of 606 known actinomycetes to determine whether any of the isolates were members of previously defined species. Only 12 of the profiles (representing 26 isolates) matched a known strain at $S_{mO} \geq 85\%$. The remaining profiles were sufficiently distinct to be considered members of different species.

The identifications produced by FAME analysis were used to construct a species table, which was then used to estimate total species diversity of the isolates and species diversity within and between the sampling sites (Table 2). A rank-abundance plot of the combined data approximates a log normal distribution with some deviation from linearity in the tail (Figure 2). This suggests that the zoosporogenous actinomycetes isolated from these soils are members of a large, mature and varied community rather than one that is under extreme stress [17]. Approximately one-third of the isolates belonged to a single *Geodermatophilus*-like species (271/826) and two-thirds of the isolates (551) could be assigned to 17 species having ≥ 5 replicates. Seven of these predominant species were identified as *Geodermatophilus*-like by FAME analysis and micromorphology. These species contained the majority of the isolates (475). Fifty-three isolates were assigned to six species of *Actinoplanes*, 17 isolates to three species of *Streptomyces* and five isolates to one indeterminate species. Among the dominant species only two of the *Streptomyces* spp matched a known culture ($S_{mO} \geq 85\%$). One hundred and six isolates were assigned

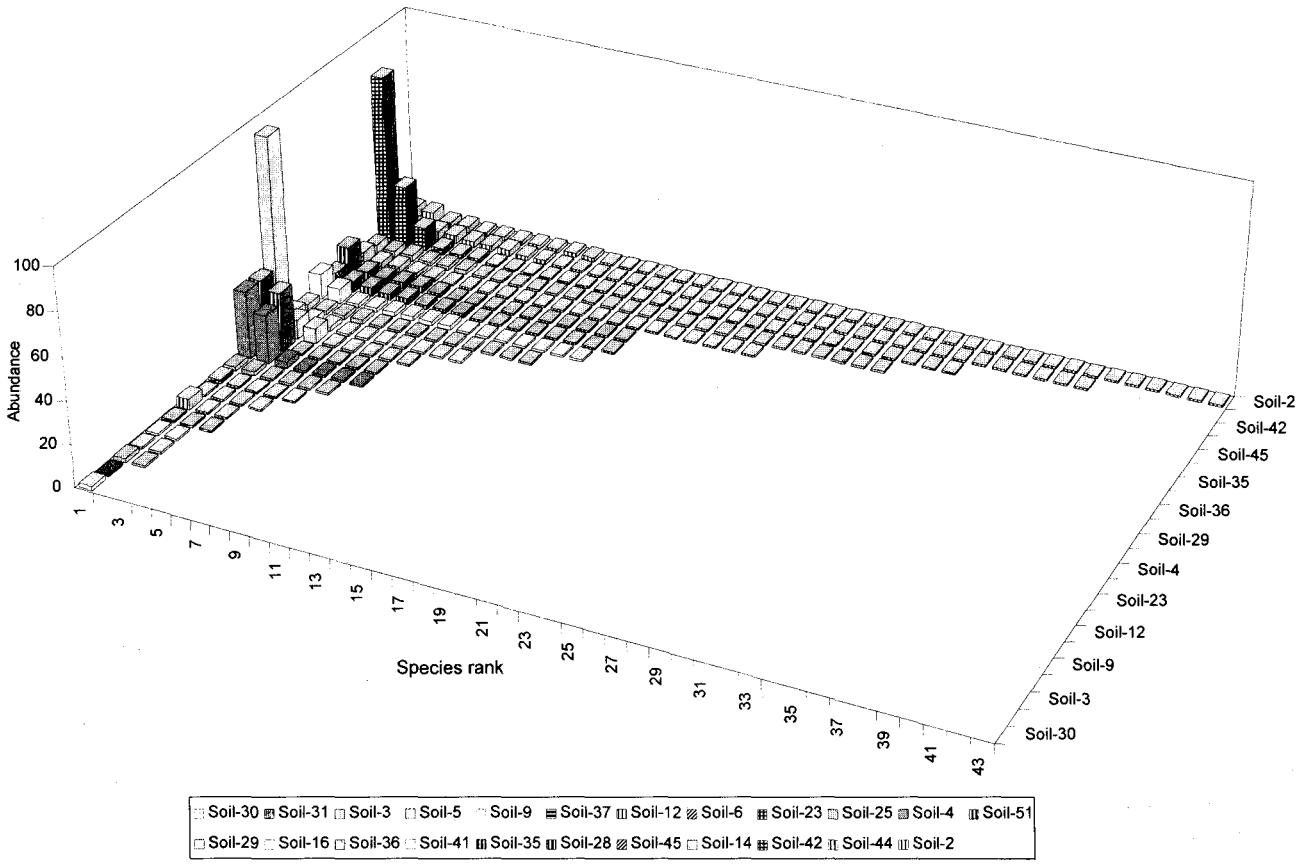

Figure 3 Site-specific rank abundance plot for zoosporogenous actinomycetes from the Mojave Desert. Data from Figure 2 were further categorized according to the soil sample from which isolates were recovered. The number of isolates assigned to each species was summed and plotted in rank order of species occurrence for each soil to depict species diversity visually.

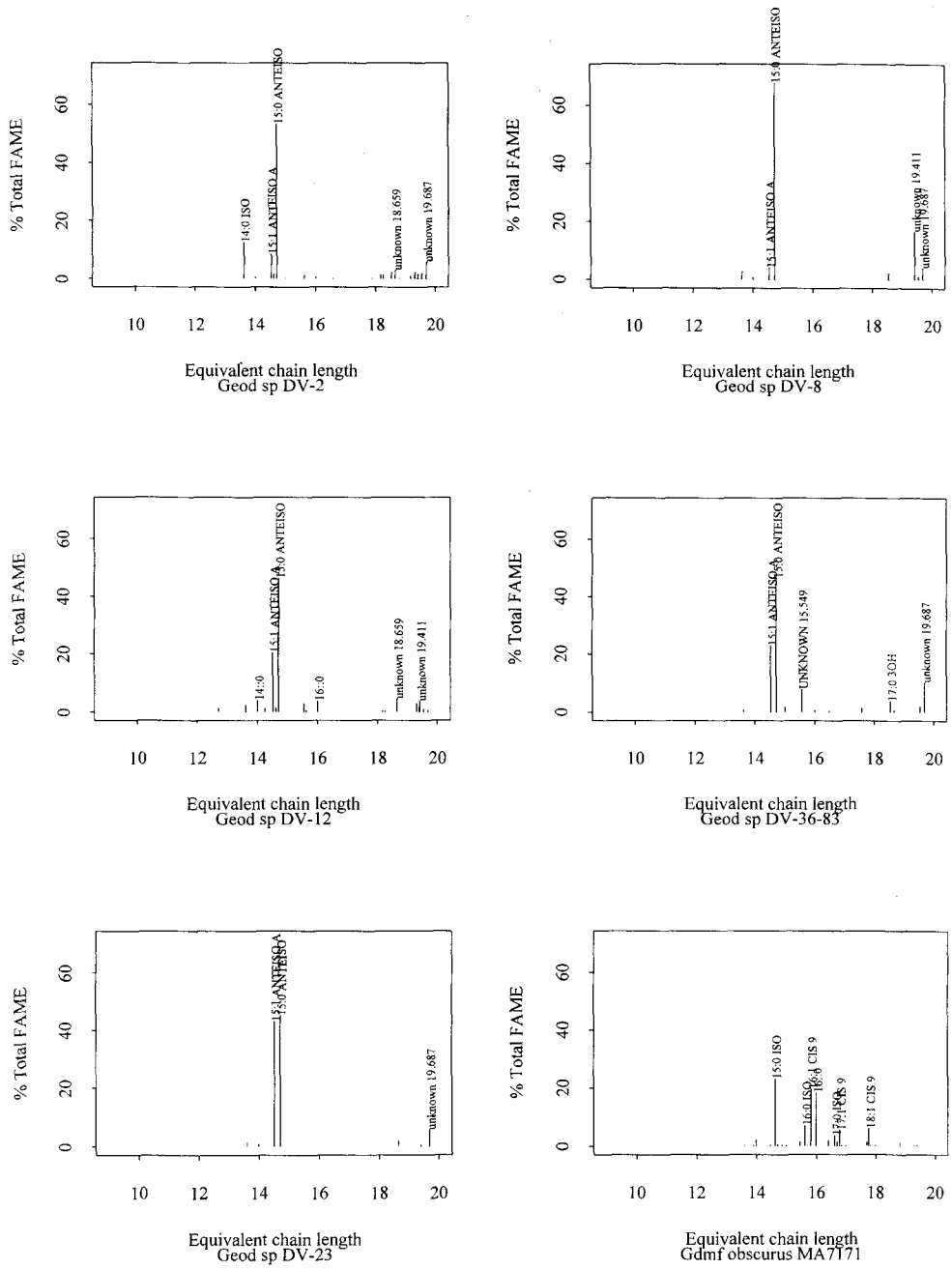

Figure 4 FAME profiles of representative biotypes of *Geodermatophilus*-like isolates and the type strain of *Geodermatophillus obscurus*. Identity of fatty acids found at concentrations exceeding 3% of the total are identified in each chromatogram.

to 39 intermediate species (2–5 isolates). The remaining 169 were all members of rare species.

When the data were examined on a site-by-site basis, marked differences in species abundance, diversity and composition were found (Figure 3). The total number of species recovered from the individual soils ranged from 1–43. The highest levels of species diversity were found in soils 42, 44 and 2 (HB = 2.84, 2.66 and 2.62; E = 0.72, 0.84 and 0.78 respectively). Further examination of the species table reveals that the asssemblages of zoosporogenous actinomycetes isolated from these soils were distinctive. These three sites each possessed a different dominant species. In soils 42 and 2, *Geodermatophilus*-like spp predominate while in soil 44 a single *Actinoplanes* sp was predominant. Several other soils also had one or two dominant species (soils 4, 51, 29; HB = 1.77, 1.79, 1.83; E = 0.59, 0.56, 0.50 respectively). The remaining soils tended to yield a much more equitable distribution of species, which is reflected in the evenness measures.

On a course level, the soils could be grouped into five general categories: those that failed to yield zoosporogenous actinomycetes; those containing *Geodermatophilus*-like isolates but not *Actinoplanes*; those in which *Geodermatophilus*-like isolates were the dominant zoosporogenous

Table 2 Abundance of species of zoosporogenous actinomycetes recovered from 29 Mojave Desert soils

Species	Soil No.																							Total
	30	31	3	5	9	37	12	6	23	25	4	51	29	16	36	41	35	28	45	14	42	44	2	
Geod sp DV-23	2	1	–	–	–	1	–	–	–	2	32	32	94	–	–	7	–	14	2	–	81	2	1	271
Geod sp DV-16	–	–	–	–	–	–	–	–	–	–	23	10	9	2	–	2	–	2	–	–	29	1	2	80
Geod sp DV-26	–	–	–	–	–	–	–	–	–	–	3	28	7	–	–	2	–	–	1	–	11	–	–	52
Geod sp DV-1	–	–	1	–	–	–	–	–	–	–	–	–	–	3	–	2	–	–	–	–	–	–	30	36
Geod sp DV-29	–	–	–	–	–	–	–	–	2	–	–	–	–	1	–	12	–	–	–	–	–	–	–	15
Geod sp DV-2	–	–	2	–	–	–	–	–	–	–	–	–	–	5	–	2	–	–	–	–	–	–	6	15
Geod sp DV-12	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	4	–	–	–	–	–	6
Rare *Geod* spp (3)	–	–	–	–	–	–	–	–	–	4	1	1	1	5	2	10	–	3	3	1	4	1	3	39
Atpn sp DV-53	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	21	–	21
Atpn sp DV-62	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	1	1	4	–	8
Atpn sp DV-74	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	1	1	–	–	8
Atpn sp DV-47	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	6
Atpn sp DV-55	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	3	–	–	6
Atpn sp DV-44	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	3	–	–	–	5
Rare *Atpn* spp (85)	–	–	–	–	–	–	–	4	–	–	2	1	–	–	3	–	–	10	11	13	10	30	29	113
Indet sp DV-62	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	1	–	2	5
Rare indet spp (69)	–	–	–	2	2	2	1	–	3	–	1	1	4	1	9	1	1	3	7	14	10	15	10	87
Stmy nogalater-like	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	–	–	–	–	–	–	7
Stmy violaceusruber-like	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	–	–	5
Stmy sp DV-85	–	–	–	–	–	–	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5
Rare *Stmy* spp (25)	–	–	–	–	–	–	1	–	1	–	–	–	–	–	1	–	23	–	2	4	2	–	2	36
Total isolates	2	1	3	2	2	3	7	4	6	8	62	74	115	17	18	38	36	39	33	38	153	74	91	826
Species	1	1	2	2	2	3	3	4	5	6	7	7	8	10	13	15	16	16	22	28	31	37	43	
HB	–	–	0.37	–	–	0.37	0.76	–	0.50	1.15	1.77	1.79	1.83	1.73	1.66	2.13	2.00	2.02	2.03	2.36	2.84	2.66	2.62	
E	–	–	1.00	–	–	1.00	0.77	–	0.67	0.98	0.59	0.55	0.50	0.95	0.94	0.87	0.85	0.81	0.88	0.96	0.72	0.85	0.78	

Numbers included in parentheses indicate the number of distinct species to which the isolates were assigned. HB is the species diversity as measured by the Brillouin Index. E is the measure of evenness.

forms; those containing *Actinoplanes* spp but not *Geodermatophilus*-like isolates; and those in which *Actinoplanes* isolates were the dominant zoosporogenous forms. There were four soils in the first category (soils 5, 9, 12 and 35), nine in the second (soils 30, 31, 3, 37, 23, 25, 29, 16 and 41), five in the third (soils 4, 51, 28, 42 and 2), one in the fourth (soil 6), and four in the fifth (soils 36, 45, 14 and 44). We are unable to find any obvious association between the species composition of a soil sample and the dominant vegetation at a particular site. From this, we infer that the species we recovered are probably free-living saprobes. We note, however, that only two *Geodermatophilus*-like isolates were found in samples collected at either freshwater or salt-water springs or streams. This suggests that there may be a negative association between soil moisture and the presence of these organisms.

Only 34 *Pilimelia*-like isolates were recovered from 8/32 soils using the baiting technique. While the total number of isolates was low, overall diversity was high. Eighteen of the isolates were unique at the S_{mO} 85% level. In the case of Soil 5, both of the isolates were recovered by this technique. The remaining isolates grouped with other *Actinoplanes* (12) or indeterminate species (4) based on the FAME profiles. *Geodermatophilus*-like isolates were not recovered using this technique. This, however, is attributed to the presence of novobiocin in the medium used to recover isolates from washed hairs following baiting. As expected, we found some overlap in the isolates recovered by baiting and chemoattraction. Approximately half the keratinophilic isolates exhibited chemoattraction to γ-collidine and/or xylose.

An unanticipated finding of this study was the recovery of the large number of *Geodermatophilus*-like strains. Although *Geodermatophilus* spp are known to be abundant in desert biomes [1,7,14] there are no reports on the recovery of these organisms using chemotactic isolation techniques. Furthermore, while morphologically similar to *Geodermatophilus obscurus* and '*Blastococcus aggregatus*', the isolates recovered from these habitats exhibited markedly different fatty acid profiles (Figure 4).

By FAME analysis, similarity of the type material of *Geodermatophilus obscurus* and *Blastococcus aggregatus* to that of the Mojave desert *Geodermatophilus*-like isolates was quite low (S_{mO} = 1.5 – 13%). The dominant lipids in the profiles of the latter were $C_{15:0anteiso}$ and $C_{15:1anteiso\ A}$. On average, these two lipids accounted for 74.2 ± 3.82% of the whole cell lipids with an equivalent chain length (ECL) of $\leq C_{20}$. In addition to the unusually high concentrations of $C_{15:0anteiso}$ and $C_{15:1anteiso\ A}$, three unidentified fatty acids with ECLs of $C_{18.659}$, $C_{19.411}$ and $C_{19.687}$ were found either singly or in various combinations and accounted for approximately 7–10% of the total fatty acid concentration. Of these five fatty acids, only $C_{15:0anteiso}$ occurs in the type strains of *Geodermatophilus* and in substantially lower amounts (0.5–2.3%). Furthermore, the type strains exhibit FAME profiles that are more like those of *Actinoplanes* spp, containing $C_{16:1\ cis\ 9}$, $C_{17:1\ cis\ 9}$ and $C_{18:1\ cis\ 9}$ in significant amounts. These three fatty acids are absent in the Mojave desert isolates. These results suggest that the *Geodermatophilus*-like strains may be members of another, previously undescribed taxon.

In conclusion, deserts are typically thought to be harsh and barren environments where relatively few organisms can survive. In reality, desert habitats are rich in flora and fauna which have specifically adapted to survival in nutrient-poor environments. Among the adaptations that permit organisms to survive under such extremes are resistance to desiccation and mechanisms for propagule dissemination. Clearly, the production of spores provides a means of long term survival for actinomycetes. The adaptations of spore motility and chemoattraction must confer additional evolutionary advantage to actinoplanetes and other zoosporogenous microorganisms found in desert soils.

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