Dictyostelids living in the soils of the Atlantic Forest, Iguazú region, Misiones, Argentina: description of new species

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Abstract: Thirteen new species and varieties of dictyostelid cellular slime molds (csm) were isolated from soils of the Atlantic Subtropical Rain Forest at the Iguazú Falls, Northeastern Misiones Province, Argentina. Seven new species are described herein, one of them is a Polysphondylium, while the rest of the species belong to the genus Dictyostelium. Also, six taxa are new varieties of Dictyostelium and Acytostelium, which will be reported later. Fourteen Northern Hemisphere (Tikal) species have also been isolated from Iguazú soils, some of them new records for Southern South America. This csm community, when compared with others from forests of the Northern Hemisphere, particularly Tikal, Guatemala, give some insight into a possibly different evolutionary history and/or natural selection in the two areas.

Key words: Dictyostelium, Polysphondylium, Southern Hemisphere, Subtropical Atlantic Forest, Taxonomy

INTRODUCTION

Dictyostelid cellular slime molds (csm) were recovered from soils of the Atlantic Subtropical Rain Forest at Iguazú Falls, NE Misiones (25° 28’ S), Argentina during 1995 and 2003 (Vadell 2003, Vadell and Cavender 1995). Seven new undescribed species and 6 new varieties along with 14 other known species and varieties represent the known portion of the community of csm in the soils of the Iguazú forest environment. There are few publications on dictyostelids of the forest soils of the Southern Hemisphere. Cavender (1969) reported the distribution of 9 species in forest soils of East Africa. Hagiwara (1973a) isolated 4 species from soils collected in Papua, New Guinea and the Solomon Islands while Cavender (1976a, b) obtained 14 species and two varieties, 5 of which were new, from subtropical and tropical Southeast Asia. Olive (1975) had reported 3 species from New Zealand, where Stephenson et al (1995) reported 7 species 20 y later. Stephenson et al (1998) recovered one species from the subantarctic Macquarie Island, Southeastern New Zealand. Cavender et al (2002) obtained 13 species, 5 of them new, from the North and South islands of New Zealand (35° 16’–46° 55’ S).

Piaggio (1989) reported the distribution of 5 species in Eastern Uruguay. Landolt & Stephenson (1991) and Cavender (1996) isolated a total of 28 species, 2 of them new (Cavender and Vadell 2000), from different collections from the Amazon basin of Peru. Vadell & Cavender (1995) and Vadell (2003) first reported on the dictyostelid research at Iguazú, Misiones, Argentina. Also, Vadell (2000) reported 7 species from the southernmost subtropical forest near the estuary of the Rio de la Plata, Punta Lara, in the Province of Buenos Aires, Argentina (34° 49’ S). A recent survey from the valdivian and Nothofagus forest of Patagonia added six out of nine still undescribed species from the southern colder regions of Argentina, between 40° and 55° S (Cavender et al 2005).

The distributions of most of the new taxa of Iguazú, appear to be confined to the Eastern Atlantic Semi-evergreen Rain Forest of South America. D. dichotomum, is strongly yellow pigmented, similar to D. granulophorum from Tikal (Vadell et al 1995), but has a dichotomous pattern of branching, also seen in D. bifurcatum, from Southeast Asia (Cavender 1976a). Among the smaller species, D. nanopodium has very small, slightly curved, uniform sorocarps. D. macrocarpum, has narrow spores with consolidated polar granules and ample domed pseudoplasmodia. D. vermiformum has small worm-like migrating pseudoplasmodia and prostrate lower sorophores. D. menorah has candelabrum shaped sorogens. D. brevicaule Olive var. brevicaule Vadell et Cavender has stout solitary sorophores and spores with small vesicles. Polysphondylium arachnoideum, the other large species, forms a network of thin terminal segments, almost spider web-like.

MATERIALS AND METHODS

Study area.—The Iguazú National Park encompasses an area of 550 km², on the left bank of the Iguazú river, a natural border between Argentina and Brazil. An additional smaller area belonging to the Iguazú Regional

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Park, is located to the west of the horseshoe shaped front of the cascades which are 2.7 km long and about 70 m tall. This connects the Iguazú National Park of Argentina and the Iguacu Regional Park of Brazil (Bailly 1995). The falls are located at 25° 28′ S, 56° 1′ W. Elevations range from about 50 to 250 m above the sea level. Soil forming bedrock is vulcanite, outcropping at the river margin. Soils in the area of Iguazú Falls are mostly lateritic (Bonfils 1970). In some localities there is a warmer microclimate in comparison to the surrounding forest of Misiones and the air is very humid due to the effect of the mist from the cascades. Mean rainfall is 1700 mm/yr and annual mean temperature is 20–21°C. Soils are well drained and rich in organic matter. The litter layer is 3–15 cm thick. Plant and animal diversity is high. Plant composition is heterogeneous, thus different habitats are found in close proximity. Detailed biogeographical data on these environments can be consulted in Cabrera & Willink (1982).

**Sampling.**—Dictyostelid csm described herein were recovered from soil and litter samples as part of Vadell’s dissertation research at the University of Buenos Aires. A majority of the sampling was carried out during Apr. 1999; Nov. 2001 and Feb. 2003, with some samples collected on other dates. Four different collecting sites within the Iguazú National Park and Iguazu Regional Park are described below. Plant nomenclature follows the flora of Dimitri (1974). (1) Site I. Upper-lower trails of the Iguazu falls within the National Park. A constant mist is characteristic of this environment with sloping gallery forest. Commonest vascular plant species are Alchornea irticifera, Apuleia leiocarpa, Arecastrum romanzeziana, Cecropia adenosia, Chusquea ramosissima, Ficus monnii and Chrysophyllum gonacarpum. Elevation varies from 69 to 150 m. Litter layer is not homogeneous in thickness, sometimes with denuded rocks and lateritic soil. Mean soil pH is 6.5 and C/N = 15.7. (2) Site II. Macuco trail, within the National Park, 2–3 kms NW from the falls. Commonest tree species are Chrysophyllum gonacarpum, Bastardiopsis densiflora, Inga uruguensis, Machaerium stipitatum, Ocotyle dioxyphylla and Luehea diversicolor. Elevation varies from 70 to 180 m. Litter is abundant. Mean soil pH is 5.8 and C/N = 14.9. (3) Site III. Yacaratai trail, 4–5 kms. NW of the falls. Commonest tree species are Aspidosperma polyneuron, Cabrala oblongifolia, Nectandra megapotamica, Ocotyle dioxyphylla, Lonchorcarpus muehlerianus, Cedrela fissilis and Tabebuia ipe. Elevation varies from 250 to below 200 m. Litter is abundant. Mean soil pH is 6.6 and C/N = 11.3. (4) Site IV. Yvy-apu trail, which is along a 60 km² area 10 km NW of the falls, within the Iguazu Regional Park. The aboriginal people, Mbyá Guarani, inhabit this environment. Commonest tree species are Aspidosperma polyneuron, Diastenopteryx sorbifolia, Para-piptadenia rigidia, Patagonula americana, Cabrala oblongifolia, Inga uruguensis. Soils are mostly lateritic with variable litter deposition. Mean pH is 6.2. Elevation is 180 m above sea level. Sites II, III and IV are fairly pristine; Site I has some anthropogenic disturbances.

**Sample processing.**—Samples of 20 g of surface humus and litter were collected in plastic bags, and stored within a cooler. Twenty of the collected samples were processed from each of the four described environments. Samples were plated out on dilute hay infusion agar media in the laboratory according to the Cavender’s isolation technique (Cavender and Raper 1965). Clones of each species were identified and presumptive new taxa were isolated and inoculated on agar media in a two membered culture with Escherichia coli B/r, under diffuse light and at different controlled temperatures. Each one of the cultures was observed every day for aggregation, pseudoplamodia and sorocarp formation and data were collected progressively. The clones recovered were studied, identified, drawn, photographed and described. Taxonomic nomenclature follows that of Raper (1984). The optical equipment used were a Bauch & Lomb dissecting microscope, an Olympus compound phase contrast microscope, a Stemy SR Zeiss and Reichert dissecting lenses. Spores, myxamoebae and sorophores of different clones were suspended in Bonner’s salt solution (Bonner 1947) for measurements under the microscope. All clones of taxonomic value were lyophilized and deposited in the BAFC (Buenos Aires Facultad de Ciencias) Culture Collection of the University of Buenos Aires and in the Kenneth B. Raper CSM Collection at Ohio University. New species were sent to the American Type Culture Collection, Manassas Virginia.

**RESULTS**

**Dictyostelium macrocarpum** Vadell et Cavender sp. nov.  
(Figs. 1A–C, 2A–H.)  
Sorocarpia culta in agaro nonnutricio cum Escherichia coli ad 12–26°C solitaria vel fasciculata, prona, irregulariter ramosa parvaque. Sorophora sinuosa, prostrata, 1–2.8 mm longa. Sorophora irregularia, gradatim attenuata e basibus multicellularibus ad apices (8–10 μm). Praesertim sorophora infra apices unicellularia nata sunt. Bases rotundae vel claviformes (15–20 μm diametro). Bases inclusa in capsula muscosa. Sori albo-hyalini, irregulariter globosi (80–200 μm diam.). Sporae ellipticae vel reniformes, angustae breves; granulis consolidatis polariibus et subpolariibus, regulares, 4–6 (–6.5) × 2–3 μm (dimidium 5.10 × 2.2 μm). Aggregatio prismo tholiformis vel tumuliformis, dein irregularis rivulis brevibus dendroides regularibus. Aggregationes partitae, centris secundariis minoribus sorogena solitaria factis; aggregaciones majores 1–2 mm in diam., minores rarissime rivulis. Sorogena praecocia usque ad 1 mm longa, plerumque vermiciformia, recurvata, regularia in diam., sinuosa; serotina longissima. Saepe sorogena elongata et vermiciformia (1 mm). Myxamoebae parvulae, 1–2 vacuolii.

Sorocarps solitarii to tightly clustered (Figs. 1C, 2C), 1–2.8 mm high, in general irregularly branched in aged cultures, sigmoid, prone, mostly with prostrate lower sorophores, when cultivated on nonnutrient agar with Escherichia coli at 22–26°C (Fig. 2H). Sorophores unevenly tapered from expanded bases to
Fig. 1. Features of Dictyostelium species from Iguazú. A–C. D. macrocarpum. A. Elliptical-reniform spores with consolidated granules. B. Ample dome-like aggregation. C. Clustered sorocarps. D–F. D. brevicaule. D. Elliptical spores with sparse vesicles. E. Late aggregations and developing sorogens. F. Unbranched stout sorocarps. G–I. D. dichotomum. G. Elliptical-oblung spores with irregularly distributed consolidated and unconsolidated granules. H. Large aggregation with secondary
tips. Terminal segment generally of one tier of cells. Tips capitate, regular, 8–10 μm diam (Fig. 2E). Bases slightly globose to clavate, 15–20 μm diam, within a mucilaginous capsule (Fig. 2D). Soris white-hyaline, globose, irregular, 80–200 μm diam. Spores elliptic to reniform, narrow, 4–6 (–6.5) × 2–3 μm, and 5.10 × 2.2 μm on average; very regular in size and shape, with consolidated polar to subpolar granules (Figs. 1A, 2G). Aggregation dome or mound-like at first, as a flattened globule, then becoming irregular and developing dendroid short regular streams (Figs. 1B, 2A). Aggregations partite; secondary smaller centers of aggregation will develop into solitary sorogens. Larger aggregations: 1–2 mm in diam. (Figs. 1B, 2A), the smaller rarely streaming. Early sorogens up to 1 mm in length (Fig. 2B), generally vermiform, recurved, regular in diam., sinuose (Fig. 2B, C). Late sorogens very elongated (Fig. 2C). Myxamoebae small, 1–2 vacuolate (Fig. 2F).

Commentary. The characteristic “honey drop” or dome-like shape of the early pseudoplasmodium which become massive and irregular is a distinguishing characteristic as well as the clustered sorocarps and small narrow PG+ spores.

Etymology. *macrocarpum*, referring to the ample and massive pseudoplasmodia.

Habitat and distribution. The species has been isolated from Macuco trail, Yacaratía and Yry-apú trails, Sites II, III and IV. In Macuco, in slightly acidic soil (pH 5.7, elevation 100 m).

Cultures examined. ARGENTINA, MISIONES: Iguazú National Park, Macuco trail, 25°28’ S, 56° 1’ W, elevation 100 m. Isolate MGE2 from soil-litter, 8 Mar 2003, Cavender 212 Y4, BAFC 1099 (HOLOTYPE), present in very pristine areas of Iguazú. Other isolations from Yacaratía trail and Yry-apú trail were observed but not preserved.

Dictyostelium brevicaule Olive var. brevicaule Vadell et Cavender sp. nov. Figs. 1D–F, 3A–I

Sorocarpia culta in agaro nonnutticico cum Escherichia coli ad 18–25 C, solitaria aut bifasciculata; erecta vel prona, rarissime ramosa parvaque e bases. Sorophora 1–3 mm longa, leve phototropica. Sorophora alba, leve curva per gradatim attenuata e basibus dilatatas ad apices. Apices capitatae (3–10 μm diam.). Bases rotundae, irregularia, ampla, saepe in plana termina (40–90 μm diam). Sori albo-hyalini, globoși (100–340 μm diam.). Sporae e ellipticae vel ovalis, saepe vesiculis, saepe 6–7.5 (–7.8) × 3–4.2 μm, et in dimidium 6.8 × 3.3 μm. Capsula spor ii partiae per symmetrica aequalia partes separant in angulo e 80 ad 90°, hiatus interporolae rectis formae; alter nexus ad termina. Aggregationes ad classe “mucoroides” pertinentes, 500–1000 μm. Sorogena vermiformia (50–200 μm), interdum abnormes. Myxamoebae saepe 2–3 vacuolae, 8–12 × 5–7 μm.

Sorocarps solitary, sometimes in loose clusters of 2–3 (Fig. 1F), erect, stout and rigid, slightly phototropic, 1–3 mm high, sometimes with short branches at or near the base, when cultivated on nonnutrient agar with *E. coli* at 18–25 C (Figs. 1F,3C, 1). Sorophores strongly tapered from expanded slimy bases to tips, slightly recurved (Fig. 1F). Tips capitate, 3–10 μm diam (Fig. 3E). Bases round to globoid, irregularly expanded, sometimes with a plane end, 40–90 μm diam (Fig. 3D). Sori globose, 100–340 μm diam., hyaline-white. Spores elliptic-ovoid, 6–7.5 (–7.8) × 3–4.2 μm, and 6.8 × 3.3 μm in average; with vesicles lobular centers and ample streams. I. Dichotomous architecture of developing sorocarp. J–L. *D. menorah*. J. Oblong-elliptical spores with dispersed consolidated granules. K. Small aggregations with developing sorocarps. L. Typical candelabrum-like architecture of the sorocarps. Bars: A, D, G, J = 5 μm; E, F = 0.5 mm; B, C, H, I = 0.5 mm.
Spores dehisce longitudinally leaving two symmetrical spore-case halves attached to one of the spore ends, at an angle of 80°–90° (Fig. 3G). Aggregation of the ‘‘mucoroides’’ type, 500–1000 μm diam. (Figs. 1E, 3A). Sorogens vermiform, sometimes peanut shaped (Fig. 3B). Myxamoebae 2–3 vacuolated, 8–12 μm (Fig. 3H).

Commentary. This species resembles that of Olive (1901) in one important respect, e.g. the short sorophore.

Etymology: brevicaule, referring to the short height of the sorocarps.

Habitat and distribution. Isolated from soil-litter at all environments searched in the Iguazú, both Regional and National Parks, presumptively common within the region from Aug to Mar (soil pH range 5.8–6.6, elevation range 100–250 m).

Cultures examined. ARGENTINA, MISIONES: Iguazú Regional Park, Yry-apú trail, 25°28’ S, 56° 1’ W, elevation 180 m. Isolate from soil-litter, 20 Aug 1999, Vadell No. 1049YA17, BACF 955 (HOLOTYPE) and ARGENTINA, MISIONES, Iguazú National Park, Site I, Upper-Lower trail, 26 Sept 1995, Vadell No. 1051CC8, BACF 957; Macuco trail, 15 Nov 2001, Vadell No. 1105M4, BACF 1127; Yacaratia trial, 8 Mar 2003, Cavender No. 4 4Y3, BACF 1158. Also isolated from soils of Puerto Canoas, Iguazú National Park in Feb 2001.

Dictyostelium dichotomum Vadell et Cavender sp. nov.

Sorocarpia culta in agaro nonnutricio cum Escherichia coli ad 20–21 C solitaria vel fasciculata, prona vel erecta, itern cum ramea aequaliter bifurcata, e semel ad quatuor, similaris ad dichotomico concepto, intense lutei, 0.6–2.5 mm longa (dim. 1.3 mm), phototropica. Sorophora lutea, irregularia: sorophora supra bases saepe prostrata, curva et prona. Apices capitates (15–25 μm diam.). Bases irregularia, ampla, saepe prostrata, e clavatae ad anomalae. Sori pallidus, globosi (80 μm diam.). Sporae capitates (15–25 μm diam.). Bases irregularia, ampla, saepe prostrata, e clavatae ad anomalae. Sori pallidus, globosi (80 μm diam.). Sporae capitates (15–25 μm diam.). Bases irregularia, ampla, saepe prostrata, e clavatae ad anomalae.
Sorocarps solitary to clustered, sinuose, erect to prone, dichotomously branched (Figs. II, 4D, L), intense yellow pigmentation, 0.6–2.5 mm (average 1.3 mm) in length, phototropic, when cultured at 20–21 C on nonnutrient agar with E. coli. Sorophores uneven, with clavate amorphous bases (Fig. 4E) (range 10–40 µm), sometimes unfinished, and within a dense matrix of slime, and compound capitate tips (Fig. 4F) (range 15–25 µm). Lower sorophores generally prostrate, curved and inclined. Sorophore architecture may show up to 4 successive forks. Sori globose, intense yellow, 30–150 µm (average 80 µm) diam. Spores oblong-elliptical, yellow, with prominent polar to subpolar granules, mostly consolidated, 4–6 (–6.5) × 2–2.5–3.5 µm (average 5.1 × 2.9 µm) (Figs. 1G, 4G). Myxamoebae small and yellow (Fig. 4H). Large aggregations are of the violaceum type, irregular, intense yellow, with lobular secondary centers of aggregation and ample streams (Figs. 1H, 4A) (range 0.6–2.5 mm). Small aggregations radiate (range 0.25–0.5 mm). Early sorogens vermiform, very elongated and sometimes bifurcated (Fig. 4B) (300–1000 µm).

Commentary. Early sorogens may migrate briefly (Fig. 4B left). Angles of bifurcation vary from nearly 180° to 90° (Fig. 4J, K). Intense yellow color of pseudoplasmodia, sorogens and sorocarps, when cultivated in darkness; slowly fades with continuous cultivation under diffuse light. Some strains produce microcysts (Fig. 4I). Below or above optimal temperatures sorocarps may not be dichotomous, or may branch irregularly.

Etymology: dichotomum referring to the dichotomous pattern of branching.

Habitat and distribution. Isolated from soil-litter of Macuco trail, Iguazu National Parks (soil pH 5.8, elevation 100 m), and also from the soil-litter surrounding the Jesuitic ruins of Loreto, Misiones, Argentina (Vadell & Cavender 1995, Vadell 2003).

Cultures examined. ARGENTINA, MISIONES: Iguazu Regional Park, Yvyapu trail, 25°28’ S, 56° 1’ W, elevation 180 m. Isolate from soil-litter, 20 Aug 1995, Vadell No. 878M9, BAFC 51182 and ARGENTINA, MISIONES, Iguazu National Park, Macuco trail, 15 Feb 2003, Vadell No. 1167M6, BAFC 834 (HOLOTYPE); Iguazu National Park, Macuco trail, Aug 1995, Vadell No. 8121GM8, BAFC 51182. ARGENTINA, MISIONES, Loreto (27° 19’ S, 55° 31’ W), Aug 1995, Vadell No. 866L9, BAFC 51157.

Dictyostelium menorah Vadell et Cavender sp. nov. Figs. 1J–L, 5A–K.

Sorocarps solitary in agar nonnutricio cum Escherichia coli ad 20–21 C solitaria vel fasciculata, erecta, ramosa, e 350 ad 550 µm longa (dim. 400 µm). Praesertim sorophora irregularia; infra apices unicellularibus nata sunt. Apices grandes, capitates (10–15 µm), saepe amorpha et flexuosis, inclusa in vagina dilatata. Bases rotundae vel claviformes (20–25 µm diam.) aut geometrica plana termina, inclusa in capsula mucosa et granulosa. Ramae breves et sustentatio parvaque. Sori hyalini, globosi (~70 µm diam.). Sporae e ovalis ad ellipticae, granulis consolidatis polaribus, saepe bipolaribus, dispersa, saepe 5–7 (~7.5) × 3–4.8 µm (dim. 5.4 × 3.7 µm). Aggregatio tipi cumuli parvuli, irregulari, 200 µm diam. Brevis sorogena praecox migrans. Provecta sorogena fasciculata, ramis similari manis forma. Myxamoebae breves, 1–2 vacuolis, saepe 9 × 7 µm.

Sorocarps solitary to clustered, erect, generally branched, 350 to 550 µm high (average 400 µm) (Figs. 1K, L; 5J). Sorophores generally uneven, terminating in one tier of cells, when cultivated on nonnutrient agar with E. coli at 20–21 C. Tips compound capitate (10–15 µm), sometimes unfinished and curved, surrounded by dense slime.
Dictyostelium nanopodium Vadell et Cavender sp. nov.

Sorocarpia solitaria culta in agaro nonnutricio cum
Escherichia coli ad 22–26 C, interdum fasciculata, remissa, 0.25–0.65 mm long., praesertim non ramosa, erecta vel prona, non phototropic, regularia et aequalis a dimensionem. Sorophora per gradatim attenuata et dilatata bases ad apices (5–9 μm), breves, leve curva vel recta, praesertim cum inferior unicellularis apices partes. Apices simple vel capitates (5–9 μm diam.). Bases rotundae interdum discoidea formae, (10–25 μm diam.). Sori albo-luteoli, globosi, irregularia (30–70 μm diam.). Sporae e ellipticae ad reniformes, 4.5–6.5 (–6.7) × 2.5–3 μm (dim. 5.6 × 2.9 μm), granulis consolidatis subpolaribus, irregularues et mox germinationem. Aggregationes cumula parvulae format, irregulares (100–300 μm), rarissime radiales. Sorogena saepe vermiformis vel curva. Myxamoebae saepe 2–3 vacuolis, 7–20 × 10–25 μm. Microcystae praesentes, media magnitude 4 μm.

Sorocarps solitary, sometimes in loose clusters, 0.25–0.65 mm high, generally unbranched, erect to prone, non phototropic, even and regular in size, when cultivated on nonnutrient agar with E. coli at 22–26 C (Figs. 6C, 7K). Sorophores tapered from expanded bases to tips, straight or slightly curved. Terminal segment of sorophores generally of one tier of cells. Tips simple to capitated, 5–9 μm diam. (Fig. 7G). Bases globoid or round, sometimes disk-shaped, 10–25 μm diam. (Fig. 7F). Sorii globose, irregular, mostly 30–70 μm diam., white-cream. Spores elliptical to reniform, 4.5–6.5 (–6.7) × 2.5–3 μm (average 5.6 × 2.9 μm), with consolidated subpolar granules, irregular in shape and size (Figs. 6A, 7I). Spores germinate immediately. Aggregation is mound-like, irregular, 100–300 μm (Figs. 6B, 7A), rarely streamed. Early sorogens synchronous when clustered and briefly migrating when solitary (Fig. 7B, C); vermiciform, uncinate or recurved (Fig. 7D), sometimes bifid (Fig. 7E). Myxamoebae 2–3 vacuolate, 7–20 × 10–25 μm (Fig. 7H). Microcysts: 4 μm (in average) (Fig. 7J).

Commentary. This small species is very uniform in height and keeps its sorocarps erect holding the viable sori for a long time.

Etymology: nanopodium, referring to the minute sorocarps.

Habitat and distribution. Dry soil-litter of Site I, Upper-lower trail (pH 6.3), Iguazu National Park, Misiones, Argentina, in 2001 and from soil-litter (pH 6.2) of Site II, Yrayapu area in 2003.

Cultures examined. ARGENTINA, MISIONES: Iguazu National Park, Upper-lower trail, 25°28’ S, 56°1’ W, elevation 150 m. Isolate from soil-litter, 15 Aug 2001, *Vadell No. 1033CSg, BACF 951 (HOLOTYPE) and ARGENTINA, MISIONES, Iguazu Regional Park, Yrayapu trail, 10 Aug 2001, *Vadell No. 1036YA24, BACF 708 and Feb 2003, *Vadell No. 1037YA 25, BAFC 1042.

Dictyostelium verniformum Vadell et Cavender sp. nov.

Sorocarpia solitaria culta in agaro nonnutricio cum *E. coli* ad 20–22 C solitaria vel fasciculata, erecta vel prostrata, rarissime ramis parvaque, saepe 0.6–1.5 mm, rarissime supra 2 mm longa. Sorophora supra base prostrata, dein erecta, non phototropica. Sorophora gradatim attenuata et basibus multicellularibus ad apices, involuta in vagina irregularue et infra apicibus unicellularibus partes. Apices capitates vel amorphus (8–15 μm). Bases breves, rotundae (8–20 μm diam.). Bases inclusa in capsula mucosa. Sori albo-hyalini, globosi aut ovi formae (60–120 μm diam.). Sporae e ellipticae ad reniformes, irregularues breves, saepe grandis granulis consolidatis alii dispersa alii parvula vel nulla, saepe 4.5–8 (–8.3) × 2.0–4.5 μm (dim. 5.8 × 3.0 μm). Aggregationes ampla aut anastomosae rivulis (400–500 μm). Ergo, praecox sorogena e cumula, coronae formant. Prorecta sorogena velox, vermiformia et cum posterum non-connexus parvi corpora.
Sorogena vermiformia longissima, libera et migrantes. Myxamoebae migrantes extra bacteriae substratum.

Sorocarps solitary to clustered, erect, sometimes prostrate or becoming decumbent, rarely branched, 0.6–2 mm, rarely more and commonly not over 1.5 mm in length, when cultivated on nonnutrient agar with *E. coli* at 20–22°C (Figs. 6F, 8H, I). Lower sorophore prostrate, then prone, when not erect (Fig. 8H). Sorophore tapered from expanded bases to tips, sometimes uneven, of one tier of cells at terminus with small round bases enclosed within a sheath capsule (8–20 μm diam), with unfinished tips, when tall (Fig. 8E); most frequently with compound capitate and expanded tips, 8–15 μm in diam (Fig. 8J) and with loose expanded bases, when

Fig. 6. Features *Dictyostelium* and *Polysphondylium* species from Iguazu. A–C. *D. nanopodium*. A. Elliptical spores with subpolar granules. B. Mound aggregations and sorocarps. C. Mature sorocarps. D–F. *D. vermiformum*. D. Oblong-elliptical spores with small granules. E. Late aggregation with vermiform sorogens. F. Mature curved sorocarps with prostrate lower sorophores. G–I. *P. arachnoideum*. G. Elliptical spores with unconsolidated polar granules. H. Forked sorogen and remains of a late aggregation. I. Portions of whorled sorocarps with recurved branches. Bars: A, D, G = 5 μm; B, C, E, F, H, I = 0.5 mm.
small. Sori hyaline-white, globose to apiculate, 60–120 μm diam. Spores oblong to elliptical, irregular, with sparse small granules but sometimes with prominent granules (Figs. 6D; 8F), in a wide range of sizes, 4.5–8 (–8.3) × 2.0–4.5 μm, mostly 5–7 × 3–3.5 μm (average 5.8 × 3.0 μm). Aggregations: ample flattened streams or fine intervowen streams which anastomose (400–500 μm diam.), then a mound or a group of mounds may form a crown of early sorogens (Figs. 6E, 8A). Sorogens develop rapidly and are short, papilla-shaped at first, then vermiform and curved, may migrate freely for some time, then they lift up, leaving behind the first formation of a lower sorophore (Figs. 6F; 8B, C, D). Late sorogens are tall, sinuose and curled with prostrate lower sorophore. Myxamoebae may migrate out of the streak of bacteria.

Commentary. On hay infusion agar and below 20 C sorogens rarely migrate and sorocarps are smaller and stouter.

Etymology: vermiformum, referring to the shape of early migrating sorogens.

Habitat and distribution. Soil-litter of the Yry-apu area (pH 6) Iguazu Regional Park, Misiones, Argentina.
**Fig. 9.** Polysphydium arachnoideum. A. Aggregation of the violaceum type. B Early sorogens. C. Early fusiform and late elongated sorogens. D. Clavate base. E. Microcysts. F. Elliptical spores with refractile unconsolidated polar granules and spore case. G. Myxamoebae. H. Detail of a whorl. I, J, K, L, M. Mature sorocarps. Bars: A–C. = 0.5 mm; D = 30 μm; E = 5 μm; F = 6 μm; G = 15 μm; H = 50 μm; I–M = 1 mm.

120 μm in diam. et laterales 20–60 μm in diam., globosi, albo-hyalini. Sporae ellipsoideae ad reniformes, 5–8 (–8.5) × 3–4.5 μm (dim. 6.7 × 3.7 μm); granulis non consolidatis polaribus, refractaria. Praecox sorogena ample, dein vermiformia. Provecta sorogena longissima et curva. Aggregations ad classem ‘violaceum’ pertinentes, 500–1000 μm. Myxamoebae breves, 8–11 × 4–6 μm, saepe 2–3 grandis vacuolis. Microcystae praesentates, media magnitudo 4 μm.

Sorocarps solitary to loosely clustered, erect to prone, sometimes prostrate, small to large, slightly phototropic, from 3 to 10–15 mm when prostrate, when cultivated on nonnutrient agar with E. coli at 20–25 C. Sorophores asymmetrical, with sharp changes of axis direction, uneven. Upper sorophores of one tier of cells, sinuose, producing delicate spider-web-like trama, sometimes without sori (Fig. 9I–M).

Bases clavate, irregular, 20–40 (Fig. 9D). Number of whorls varying from 1 to 20, with internode distance of 150–350 μm, consisting of 2–4 branches of 90–230 μm. Large branches in a whorl are at 90° with respect to the sorocarp, then recurved (Figs. 6I, 9H). Lower sorophore with branches of 200–1000 μm, sometimes with secondary whorls. Terminal segment elongated and irregular, varying from 100 to 1000 μm, very thin (1.5–4 μm). Terminal sori hyaline-white, globose, 40–120 μm diam. Lateral sori 20–60 μm diam. Spores elliptical to reniform, 5–8 (–8.5) × 3–4.5 μm (average 6.7 × 3.7 μm) with refractile unconsolidated polar granules (Figs. 6G, 9F). Early sorogen expanded, then vermiform (Fig. 9C). Late sorogens very elongated and curved (Fig. 9C). Aggregation of the ‘violaceum’ type (i.e., the initial primary aggregation divides into smaller secondary centers of aggregation), 500–1000 μm. Streams are thin and elongated, sometimes ample at the edge of the aggregation (Figs. 6H, 9A). Myxamoebae small, 8–11 × 4–6 μm, generally with two large vacuoles (Figs. 9G). Microcysts: 4 μm on average (Fig. 9E).

**Commentary.** Size variation depends on both temperature and hydric conditions of the cultures in addition to the food supply. This species prevails over other dictyostelids in the Iguazu region.

**Etymology:** arachnoideum, referring to the production of a spider web-like terminal sorophores.

**Habitat and distribution.** Soil-litter of the Site I, Upper-Lower trail, Site II, Macuco trail and Yacaratia trail of the Iguazu National Park and in soils of the Yy-apu area, site IV (pH 6) Iguazu Regional Park, Misiones, Argentina. Also in Puerto Canoas, Iguazu National Park in Nov 1995. The species appears dominant in 3 sites of the Iguazu area, within the Regional and National Parks. (Vadell 2003).

**Cultures examined.** ARGENTINA, MISIONES: Iguazu Regional Park, Yy-apu trail, 25°28′ S, 56° 1′ W, elevation 180 m. Isolate from soil-litter, 17 Aug 1999, Vadell No. 1040YA7, BAFC 945 (HOLOTYPE). ARGENTINA, MISIONES: Iguazu National Park, Macuco trail, elevation 200 m. Isolate from soil-litter, 15 Nov 2001, Vadell No. 1138M10, BAFC 946. ARGENTINA, MISIONES: Iguazu National Park, Yacaratia trail, elevation 200 m. Isolate from soil-litter, 18 Nov 2001, Vadell No. 1148M15, BAFC 948.

**DISCUSSION**

The data obtained from Iguazu make possible a comparison of Neotropical dictyostelids from the Northern and Southern Hemispheres. Considerable dictyostelid data are available for Tikal National Park, Peten, Guatemala which is located in the Northern Hemisphere (Holmes 1991, Vadell 1993, Cavender 2005). Iguazu and Tikal have many similarities. Both are relatively pristine areas of sub tropical seasonal rain forest. Tikal National Park is 200 km² at latitude 17 N while Iguazu is 550 km² at 25 S. Both are surrounded by even larger areas of intact forest (Tikal 576 km², Iguazu 670 km²). The area sampled at Tikal...
Twenty seven species and varieties of dictyostelids have been isolated from Tikal, while twenty seven were found at Iguazú (both from 80–90 samples), also with a high degree of csm species richness. In addition to the seven new species reported here there are six new varieties of these existing species: *Dictyostelium lavandum*, *D. tenue*, *D. discoideum*, *D. macrocephalum*, *Polysphondylium asymmetricum* and *Acytostelium aggregatum*. The varieties differ from the described species in some important morphological feature, e.g. the variety of *D. lavandum* (Raper and Fennell 1967) lacks the crampon base but is identical in other respects. Of these species *Dictyostelium lavandum*, *D. discoideum* and *A. aggregatum* are not reported from Tikal. The first two occur in Costa Rica (Cavender and Raper 1968) while *A. aggregatum* was found in the Peruvian Amazon (Cavender 2005). Of the new species and varieties only the variety of *D. macrocephalum* (Hagiwara et al 1985) occurs at Tikal. This variety appears to be widespread in the Neotropics. There are, as a result, 15 species and varieties common to both Iguazú and Tikal: *D. polypephalum*, *D. aureo-stipes*, *D. implicatum*, *D. tenue*, *D. coerules-stipes*, *D. macrocephalum*, *D. macrocephalum n. var.*, *D. monochasioides*, *D. medusoides*, *D. purpureum*, *D. giganteum*, *D. mucoroides var. stoloniferum*, *Polysphondylum violaceum*, *P. asymmetricum* and *P. colligatum*. Therefore twelve species and varieties (44%) at Iguazú are not found to date at Tikal or elsewhere in the Northern Hemisphere. Differences in community composition between Northern and Southern Hemisphere may indicate that there is different evolutionary history and/or different natural selection factors in the two hemispheres. Other recent data may support this hypothesis. In Tierra del Fuego and Patagonia, Argentina, six of the nine species isolated are not found in the Northern Hemisphere (Cavender et al 2005). Of 13 species from New Zealand four were not in the Northern hemisphere (Cavender et al 2002) while collections from Australia show that a large portion of the species are different from those of the Northern Hemisphere (Landolt et al 2005).

In addition to the species differences there are some differences in the morphologies of the two Hemispheric groups. For example, the bases of Southern Hemisphere species are more likely to be surrounded in a dense matrix of slime. The soroi are also more likely to contain dense slime that does not allow the spores to disperse in water. The most striking difference noted however, is in the polar granule(PG) characteristic of spores. There are more species with polar spore granules in the Southern Hemisphere. For example, the percentage of PG+ species in Ohio is 42% (Cavender and Vadell 2006), in Tikal 58% (Cavender 2005), and in Iguazu 64%. The percentage of PG+ species in Australia (unpublished data) appears to be even higher at 68%. Recent molecular studies of the SSU rRNA and alpha-tubulin gene in the described dictyostelid species and the construction of a phylogenetic tree (Schaap et al 2006) shows that the PG+ species are closer to the root of the tree. The greater number of PG+ species in the Southern Hemisphere may indicate that early evolution of the dictyostelids took place there.

The seven new species described exhibit some new and interesting morphological features. *Dictyostelium dichotomum*, which is intensely yellow in pigmentation not unlike *D. mexicanum* (Cavender et al 1981) and *D. granulophorum* (Vadell et al 1995), constructs a fruiting body by means of repeated dichotomous branching. Only a single dichotomous branching has been described previously for *D. bifurcatum* (Cavender 1976a). *Polysphondylum arachnoides* produces elongated sorophore tips not unlike those of *P. candidum* (Hagiwara 1973b) however it has a much greater tendency to do this forming a web-like structure in aggregate. *Dictyostelium menora* is unusual because of the irregular branching pattern, but always resembling a candelabrum. Sometimes a number of short branches are unilateral, producing a structure much like a menora in appearance. It was isolated with what appears to be a symbiotic Actinomycete associate. *Dictyostelium macrocarpum* has relatively large mounded pseudoplasmodia, a type not seen before in dictyostelids but now discovered in this species and at least one other undescribed species from Australia (Landolt et al 2005). *Dictyostelium brevicaule* was first described by E. W. Olive (1901). Emphasis was placed in the description on the relatively short stalk in respect to the size of the sorus. Although the holotype was lost this feature is well expressed by the new variety we describe. *Dictyostelium vermiformum* has two features which set it apart, the elongated sorogens which tend to produce prostrate lower sorophores not unlike those of *D. sphaerocephalum* (Raper 1984) and the small, narrow PG+ spores. Of all the species *D. nanopodium* is the most diminutive. It is noteworthy because of its very small size, approaching *D. diminutivum* (Ander-
son et al. 1968) in stature, although there are differences from this species in the size and shape of the spores as well as the sorocarps.

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