

Taxonomic status of the genera *Sorosporella* and *Syngliocladium* associated with grasshoppers and locusts (*Orthoptera: Acridoidea*) in Africa

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The occurrence of disease outbreaks associated with the genus *Sorosporella* on grasshoppers and locusts (*Orthoptera: Acridoidea*) in Africa is reported. Infected hosts, representing ten genera within five acridoid subfamilies, are characterized by red, thick-walled chlamydospores which completely fill the cadaver. On selective media, the chlamydospores, up to seven-years-old, germinated to produce a *Syngliocladium* anamorph which is considered to be undescribed. The new species *Syngliocladium acridiorum* is described and two varieties are delimited: var. *acridiorum*, on various grasshopper and locust genera from the Sahelian region of West Africa; and, var. *madagascariensis*, on the Madagascan migratory locust. The ecology of these insect-fungal associations is discussed. *Sorosporella* is treated as a synonym of *Syngliocladium*.

INTRODUCTION

Between 1990 and 1993, surveys for mycopathogens of orthopteran pests were conducted in Africa and Asia as part of a multinational, collaborative project for the biological control of grasshoppers and locusts of the family *Acridoidea* or *Acrididae* (Kooyman & Shah 1992). These include some of the world's most destructive agricultural pests, with the most damaging, the plague or migratory species, collectively being referred to as locusts.

During the early surveys in Mali, grasshopper cadavers were collected with characteristic red, dry and powdery infections. The causal agent of the disease outbreak on nymphs of *Kraussaria angulifera* was identified as belonging to the genus *Sorosporella*, typified by brightly coloured or pigmented chlamydospores (Samson, Evans & Latge 1988), and an associated conidial state was isolated in culture (Shah 1993). Subsequent surveys in West Africa revealed the same fungus on a number of other acridoid genera (Shah *et al.* 1994, Shah, Kooyman & Paraíso 1997). Parallel surveys in Madagascar showed a similar disease on the African migratory locust which also produced a conidial anamorph *in vitro* (Welling *et al.* 1995). Shah & Evans (1997) briefly reported on these findings and expressed reservations about the taxonomic status of the genus *Sorosporella* and its associated but poorly defined

synanamorph, *Syngliocladium* Petch. Subsequently, Hodge, Humber & Wozniak (1998) described two *Syngliocladium* species from the USA and emended the generic diagnosis, which also included *Sorosporella* as a chlamydosporic synanamorph.

Based on these recent developments, the taxonomic status of the collections on African locusts and grasshoppers is re-assessed and the ecological implications are discussed.

MATERIALS AND METHODS

The techniques employed for the survey and collection of diseased orthopterans have been described earlier (Kooyman & Shah 1992, Shah *et al.* 1997).

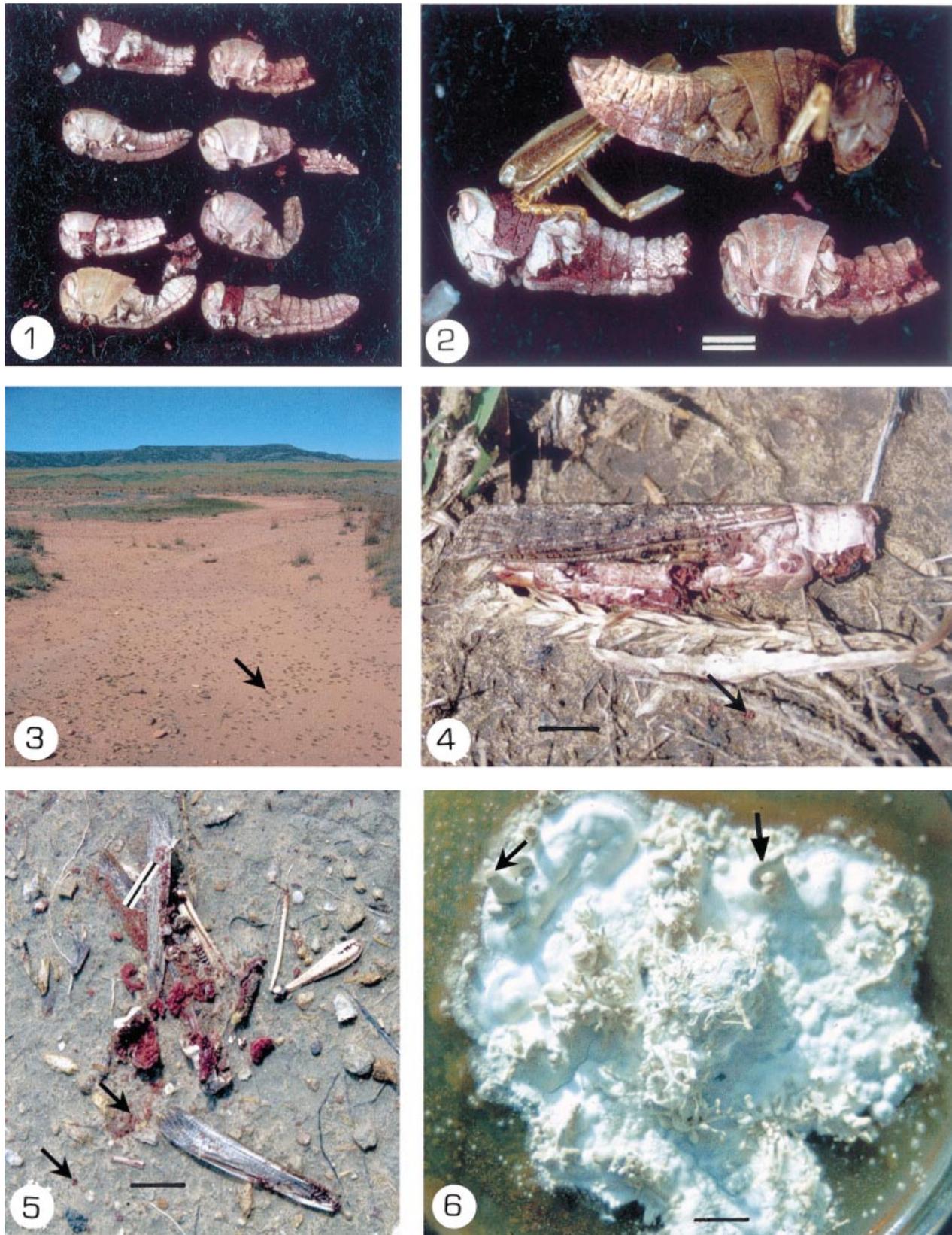
Isolations were made either by aseptically removing chlamydospore masses from host cadavers and streaking them onto agar media or by shaking the cadavers directly over the exposed agar plates containing: mealworm agar (MWA; Samson & Evans 1974); potato carrot agar (PCA) amended with cycloheximide; or, a selective medium (VMA) for detecting *Verticillium* chlamydospores in soil (Christen 1982). Subcultures were maintained on PCA, MWA and Molisch's agar (MOA) (Speare 1920), at 25 °C, with a 12 h black light cycle.

ECOLOGY

Infected orthopterans, characterized by red-coloured, mummified cadavers, were collected in the West African countries of Benin, Chad, Niger and Mali (Figs 1, 2), as

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Figs 1–6. *Syngliocladium acridiorum* on African grasshoppers and locusts. **Figs 1–2.** *S. acridiorum* var. *acridiorum* on nymphs of *Kraussaria angulifera* from Mali (IMI 386212). Note brittle condition of the cadavers, in which the appendages and sclerites are frequently missing exposing the red, powdery masses of chlamydospores. Bar = 10 mm and 5 mm respectively. **Fig. 3.** Area of collection in south-west Madagascar of locusts infected with *S. acridiorum* var. *madagascariensis*. Arrow shows a band of hoppers or nymphs migrating across the savannah. **Figs 4–5.** *S. acridiorum* var. *madagascariensis* (IMI 386216) *in situ* on adults of *Locusta migratoria capito*. Cadavers occur directly on the soil surface and slowly disintegrate to liberate irregular masses of chlamydospores (arrowed). Bar = 10 mm. **Fig. 6.** *S. acridiorum* var. *madagascariensis* *in vitro*, isolated from chlamydospores of IMI 386216; seven-month-old culture on MWA showing white, convoluted stromatic colony producing abundant synnematal initials and mature synnemata (arrowed). Bar = 15 mm.

Table 1. Hosts of *Syngliocladium acridiorum* var. *acridiorum* recorded from grasshoppers and locusts in West Africa, 1990–93.

Acridoidea	Benin	Chad	Mali	Niger
Acrididae				
<i>Oedopodinae</i>				
<i>Acrotylus blondeli</i> ¹			+	+
<i>Gastrimargus africanus africanus</i>	+			
<i>Oedaleus nigerensis</i>				+
<i>Oedaleus senegalensis</i> ²			+	
<i>Cyrtacanthacridinae</i>				
<i>Anacridium m. melanorhodon</i> ²		+		
<i>Kraussaria angulifera</i> ¹		+	+	
<i>Ornithacris cavroisi</i>	+			
<i>Cantantopinae</i>				
<i>Diablocatantops axillaris</i> ¹	+	+		
<i>Hemiacridinae</i>				
<i>Hieroglyphus daganensis</i> ¹	+		+	
<i>Pyrgomorphidae</i> (syn. <i>Pyrgomorphinae</i>)*				
<i>Pyrgomorpha cognata</i> species complex	+	+	+	+

¹ Species of slight or occasional economic importance.

² Aggregating grasshopper or locust species of great economic importance.

* Recognised as a subfamily by Johnston (1956), but as a separate family by Dirsh (1965).

well as from the island of Madagascar (Figs 3–5). These represented ten different genera within five subfamilies of *Acridoidea* (Table 1). The African migratory locust occurs as two distinct subspecies but, significantly, no infections were recorded on the mainland type, *Locusta migratoria migratorioides* which is endemic to the Niger floodplain. In contrast, the only collections of the pathogens from Madagascar were made from the subspecies unique to the island, *L. m. capito*. Infected locusts were found in the south-west region from 1992–93 (Welling *et al.* 1995), and again in 1997 (H. C. Evans, unpubl.; Sakahara, April 1997), where this species is a major pest of annual crops. In the Sahelian region of West Africa, *Oedaleus senegalensis* (Senegalese grasshopper) is now the principal pest of rain-fed cereal crops, whilst several of the other aggregating species, such as *Hieroglyphus daganensis* (rice locust), *Anacridium melanorhodon* (tree locust) and *Kraussaria angulifera* have also attained pest status in recent years (Jago 1990).

Field symptoms have been described and illustrated in detail for disease outbreaks on West African grasshoppers (Shah & Evans 1997). Typically, the cadavers are found attached to the lower vegetation in the early stages but, later, these often fall to the soil. However, the locust cadavers in Madagascar always occurred on the soil surface in various stages of degradation (Figs 4–5). There was no evidence of the summit disease behaviour, so symptomatic of acridoids infected with *Entomophaga grylli* (Fresen.) Batko (Samson *et al.* 1988). Weathering of the cadavers results in the brick-red chlamyospore masses (Fig. 5), or aggregations (Speare 1920), or agglutinations (Welling *et al.* 1995), being exposed and released onto the vegetation and soil. None of the many hundreds of

diseased grasshopper specimens examined from West Africa and Madagascar, showed any external fungal structures and it would appear that the only spore type produced on the host in the field is the endogenous, resting or chlamyospore stage, assignable to the genus *Sorosporella*. Plating of the chlamyospores, from specimens collected up to seven-years previously and stored at 20–23 °, resulted in the production of slow-growing colonies bearing conidiogenous structures as described and illustrated by Speare (1920) and Pendland & Boucias (1987) for a *Syngliocladium* synanamorph associated with *Sorosporella* infections of moths (*Lepidoptera: Noctuidae*) and mole crickets (*Orthoptera: Gryllotalpidae*) respectively.

TAXONOMY

Morphologically, the West African isolates can be distinguished from previously described *Syngliocladium* species (Hodge *et al.* 1998), and from the Madagascan isolates. However, because of the overall similarities of the pathogens associated with acridoid hosts, separation at the varietal level is recommended. The new species, *Syngliocladium acridiorum* is therefore proposed with two varieties.

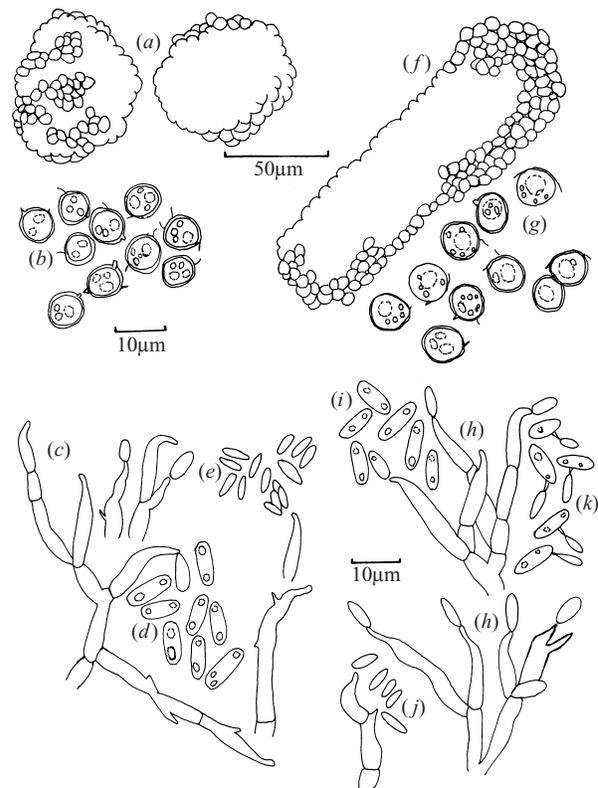


Fig. 7. *Syngliocladium acridiorum*. (a–e) var. *acridiorum* (IMI 386212). (a) Chlamyospores aggregated into discrete balls or sclerotia; (b) chlamyospores; (c) conidiophores; (d) macroconidia; (e) microconidia. (f–k) var. *madagascariensis* (IMI 386215): (f) chlamyospores, aggregation or agglutination; (g) chlamyospores; (h) conidiophores; (i) macroconidia; (j) microconidia; (k) macroconidia producing microconidia directly. Bars = 10 μm.

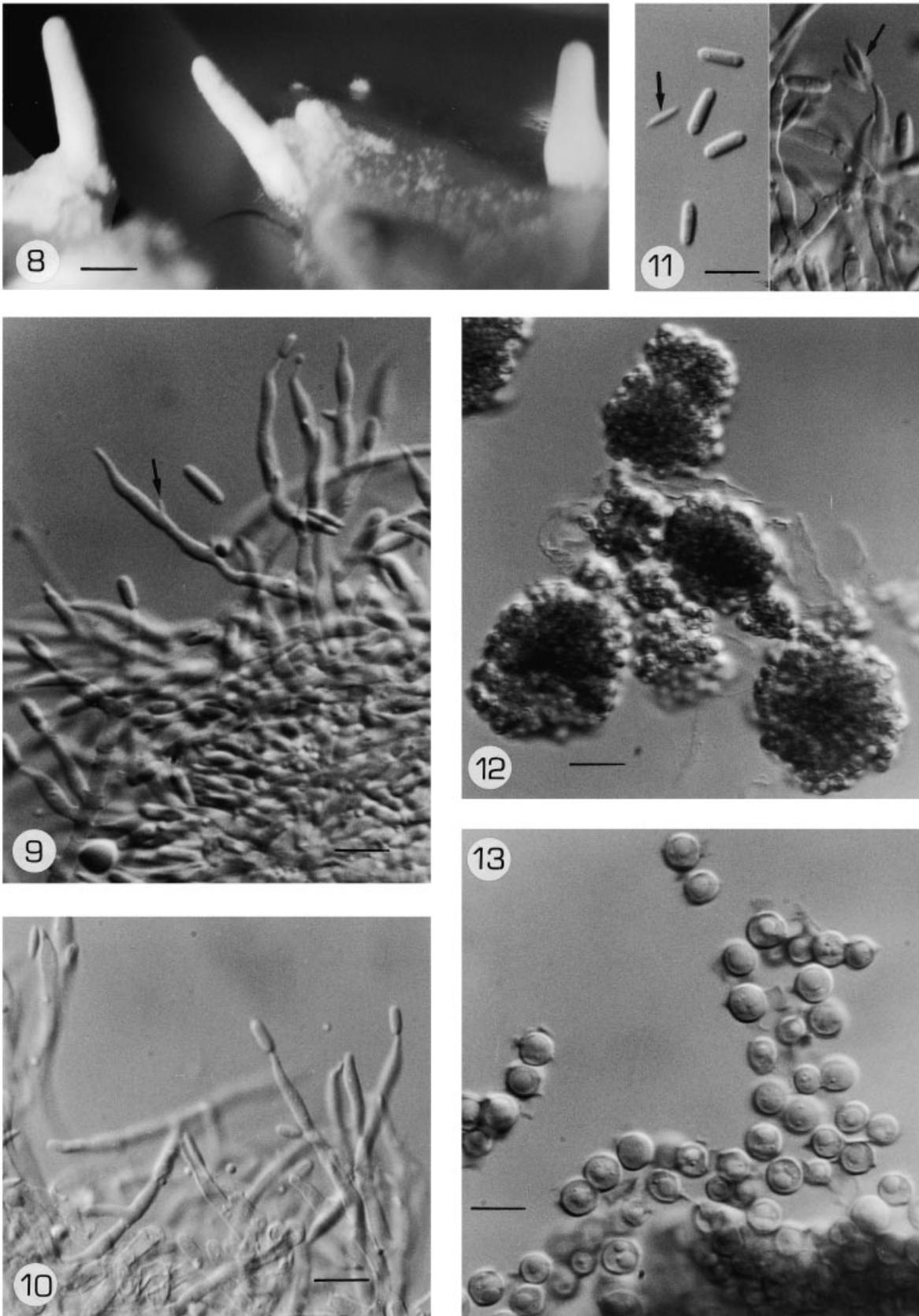


Fig 8–13. *Syngliocladium acridiorum* var. *acridiorum* (IMI 386212). **Fig. 8.** Synnemata produced on PCA after 10 weeks. Bar = 1.5 mm. **Fig. 9.** Conidiophores from a synnema showing production of macro- and microconidia and polyphialidic conidiogenous cell (arrowed; see also Fig. 7c). **Fig. 10.** Phialides on aerial mycelium. **Fig. 11.** Macro- and microconidia (arrowed). **Fig. 12.** Chlamydospore aggregations or sclerotia. Bar = 25 μ m. **Fig. 13.** Chlamydospores. Bar = 10 μ m in Figs 9–11 and 13.

Syngliocladium acridiorum H. C. Evans & P. A. Shah,
sp. nov. (Figs 1–2, 7a–e, 8–13).

var. acridiorum

Habitus entomogenus: mycelium et hyphis sporogenus externum absens. *Chlamydosporae* vel sporaes quiescentes endogenae formantes; globosae, 5.0–6.5 µm, lateritiae, crassitunicati, guttulae, interdum apiculatae, in sclerotia aggregatae; *sclerotia* subglobosa, 65–75 × 55–65 µm, pulverescens. *Coloniae* mononematosaes vel synnematosaes, albae vel rosadae, humiles, convolutescens, stromatescens; in agar PCA lentissime crescentibus, circa 1.3–1.5 cm diam post 35–40 dies and 25 °C *Conidiophoris* in mycelium et synnemata efferentibus. *Synnemata* alba vel rosada, clavata, 2–5 × 0.5–0.8 mm. *Cellulae conidiogenaes* phialidicae, solitariae vel geminatae, lageniformes vel subulatae, 12–20 (–24) × 2.5–3.5 µm saepe polyphialidicae; basibus subcylindricis in collum curvum descrescentibus, apicibus interdum uncinatibus. *Conidia* dimorphica in capitula mucida formantia: *macroconidia* aseptata, hyalina, guttulata, cylindrica vel subcylindrica, 6.5–8 (–10.5) × 2.5–3.5 µm; *microconidia* aseptata, hyaline, fusiformi, 4.5–6.5 × 1–1.5 µm. Status teleomorphicus ignotus.

Typus: **Mali**: prope lectus Mourdiah, Nara District, ex insectis acrididis (*Kraussaria angulifera*), Aug. 1990, P. A. Shah (IMI 386212 – holotypus).

Entomogenous or entomopathogenic: external mycelium and sporing structures absent. *Chlamydosporae* or resting spores produced within the host; globose, 5.0–6.5 µm, brick-red, thick-walled, guttulate, occasionally apiculate; aggregating in powdery, subglobose (65–75 × 55–65 µm) to irregular masses or sclerotia.

Colonies mononematous or synnematous, brilliant white to pale pink, low at first becoming convoluted and stromatic; very slow-growing, reaching 1.3–1.5 cm diam after 35–40 d on PCA at 25 °C. *Conidiophores* developing directly on the mycelium and on synnemata. *Synnemata* white to pink, clavate, 2–5 × 0.5–0.8 mm. *Conidiogenous cells* phialidic, solitary or in pairs, flask-shaped to subulate, 12–20 (–24) × 2.5–3.5 µm, often polyphialidic, with a subcylindrical base narrowing abruptly to a short, tapering neck, occasionally bent or hooked. *Conidia* produced in slimy heads and of two types: *macroconidia* aseptate, hyaline, guttulate, cylindrical to subcylindrical, 6.5–8 (–10.5) × 2.5–3.5 µm; *microconidia* aseptate, hyaline, fusiform, 4.5–6.5 × 1–1.5 µm. Teleomorph unknown.

Additional material examined: **Niger**: Sahoré, Niamey, on *Ornithacris cavroisi* (Acrididae), Sept. 1990, C. Kooyman (IMI 386213). **Benin**: Malanville, Fabana, on *Hieroglyphis daganensis* (Acrididae), Oct. 1992, P. A. Shah (IMI 386214).

var. madagascariensis H. C. Evans & P. A. Shah, var. nov. (Figs 4–6, 7f–j, 14–20)

Chlamydosporae 5.5–7.5 µm; non sclerotia formante, non pulveraceus. *Macroconidia* (7–) 8–10.5 (–11.5) × 2.5–3.5 µm; *microconidia* 4–5.5 × 1–1.5 µm.

Typus: **Madagascar**: prope lectus Betioky, ex insectis acrididis (*Locusta migratoria capito*), Apr. 1992, M. Welling *et al.* (IMI 386215 – holotypus).

Chlamydosporae 5.5–7.5 µm; not forming sclerotia, not pulverulent.

Macroconidia (7–)8–10.5 (–11.5) × 2.5–3.5 µm; *microconidia* 4–5.5 × 1–1.5 µm.

Additional material examined: **Madagascar**: Sakahara, isolated from *L. migratoria capito*, 1997, H. C. Evans & R. H. Reeder (IMI 386216).

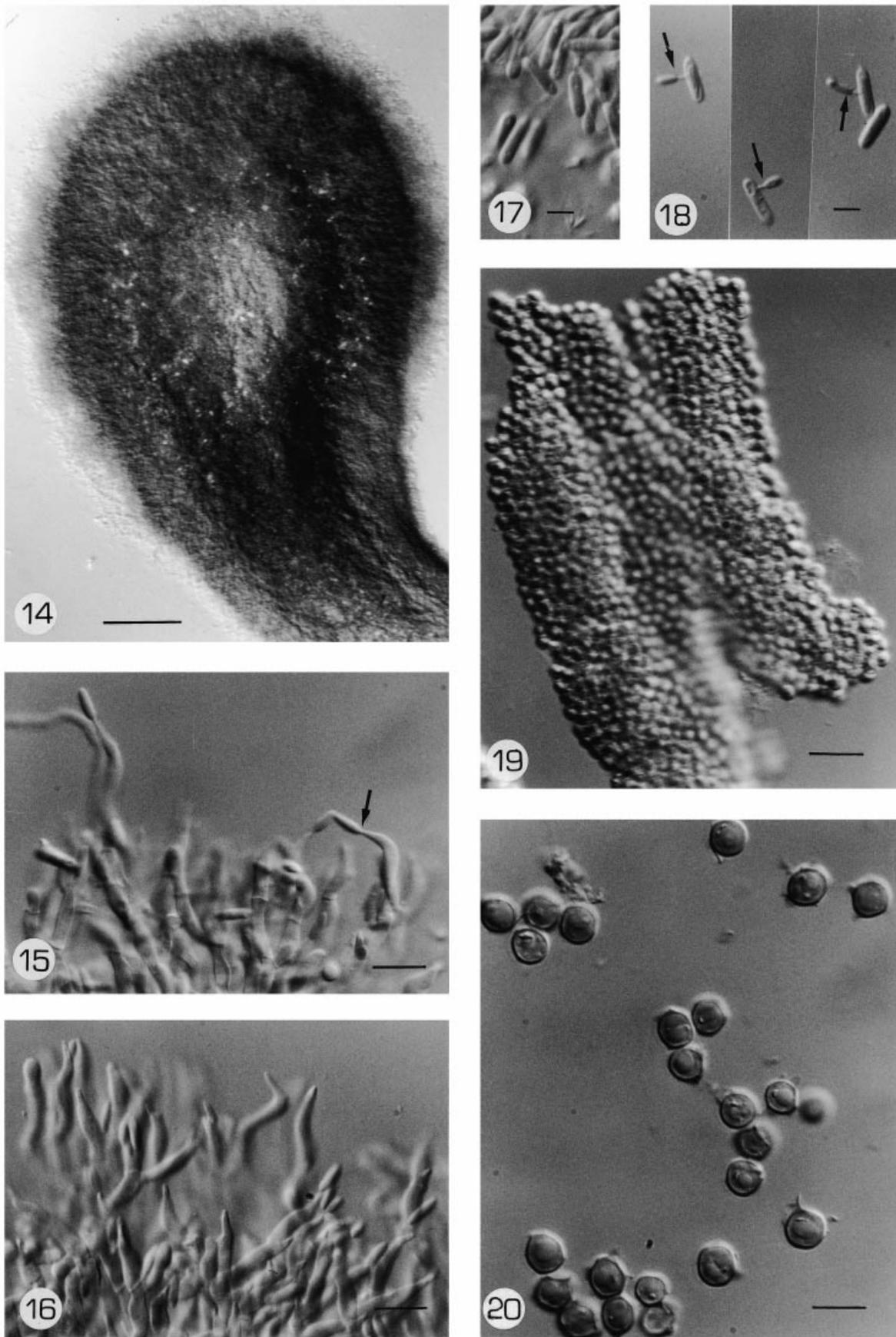
The main distinguishing character between the two varieties is the form and production of the chlamydosporae. In all the specimens of var. *acridiorum* examined, the chlamydosporae fill the entire body and readily break apart into discrete, powdery, predominantly globose, sclerotial-like bodies (Figs 7a, 12). In contrast, the chlamydosporae of var. *madagascariensis* are formed typically beneath the sclerites, running between the exoskeleton and the integument in longitudinal rows. These are not easily detached and still adhere in irregular sheets when eventually released from the disintegrating cadaver (Figs 7f, 19). Differences in spore dimensions, although these are relatively minor, further justify separation of the collections from West Africa and Madagascar. As previously noted, although the African migratory locust is endemic in West Africa, no infections have been recorded on this host despite intensive surveys (Shah *et al.* 1997).

Pendland & Boucias (1987) conducted SEM and TEM studies of the chlamydosporae of *Sorosporella* from mole crickets and showed them to be covered by a film of dark-staining, amorphous material. This layer imparts an uneven appearance to the spore surface (Fig. 7b, g), and may represent mucilaginous remnants, which served to bind the spores together.

In culture, the two varieties differ slightly in growth rate and form, although colony morphology is also variable within an isolate, due to frequent sectoring. Synnemata, when produced, are more abundant in var. *madagascariensis* and tend to be capitata (Fig. 14) compared to the clavate form of var. *acridiorum* (Fig. 8). In addition, microconidia occur more regularly in var. *acridiorum*, particularly on the synnemata, whilst in var. *madagascariensis* these appear to be produced mainly following secondary conidiation (Figs 7j, 18), analogous to the process described for some species of the entomopathogenic genus *Aschersonia* (Evans 1994).

DISCUSSION

The initial taxonomic assessment of the isolates from infected grasshoppers and locusts in West Africa and Madagascar was that they should be accommodated in a genus close to the genera *Tolypoocladium* (Gams 1971) and *Paraisaria* (Samson & Brady 1983), and that their inclusion in the genus *Syngliocladium* was debatable (Shah & Evans 1997), since the type was described from a spider host lacking any evidence of the distinctive chlamydosporae stage (Petch 1932). Subsequently, Petch (1942) expanded the generic concept to include species with *Sorosporella* synanamorphs. More recently, Hodge



Figs 14–20. *Syngliocladium acridiorum* var. *madagascariensis* (IMI 386216). **Fig. 14.** Capitate synnema produced on MWA, longitudinal section, Bar = 250 μ m. **Figs 15–16.** Conidiophores from a synnema showing phialidic conidiogenous cells, occasionally with slightly hooked or bent necks (arrowed). **Fig. 17.** Macroconidia. **Fig. 18.** Macroconidia showing microconidiation (arrowed). **Fig. 19.** Aggregations of chlamydospores. Bar = 25 μ m. **Fig. 20.** Chlamydospores. Figs 15–18 & 20, Bar = 10 μ m.

et al. (1998) accepted this conclusion and emended the generic description, since the '... creation of superfluous anamorph genera is to be avoided'. This line of reasoning is followed here, although the status of the genus can only be satisfactorily resolved by molecular characterization. However, it is considered that the distinctive chlamydospore state should be included as species characters within *Syngliocladium*, as treated here, and that *Sorospora* should be regarded as a synonym rather than a synanamorph. For example, several species of *Hirsutella* produce characteristic chlamydospores which may aggregate into pigmented spore balls, as in the case of *Synnematium jonesii* which was reduced to synonymy with *Hirsutella* by Evans & Samson (1982), or into more differentiated, sclerotial-like bodies; produced externally in *H. subramanianii* (Samson & Evans 1985), and internally in *H. cryptosclerotium* (Fernández-García, Evans & Samson 1990). None of these states are now interpreted as synanamorphs but as specialized resting or survival structures.

Speare (1917, 1920) included Sorokin's original description and illustration of the genus *Sorospora* (Sorokin 1888) in his studies and noted that no other spore stages were depicted and that there was no attempt to interpret the life-cycle of the fungus. Speare (1920) and Pendland & Boucias (1987) showed that the chlamydospores function as resting spores and germinate to produce the conidial anamorph which represents the infective stage. The chlamydospores themselves proved to be non-infective in bioassays (Shah 1993, Welling *et al.* 1995).

Cordyceps-infected arthropods invariably contain thick walled, lipid-filled hyphal bodies or chlamydospores, especially in the abdomen, from which the anamorphs of difficult-to-culture species have been obtained *in vitro* (Evans & Samson 1982). These authors used hyphal-body morphology as an additional tool in the taxonomy of *Cordyceps* spp. associated with ants and considered that these structures function as a food reserve to allow for rapid stromatal growth when favourable climatic conditions prevail. For *Syngliocladium acridiorum*, it would seem that these hyphal bodies have taken on a wider, multifunctional role in the life-cycle, since the anamorph is never produced on the host; ensuring both long-term survival as well as dissemination of the pathogen. The powdery, potentially air-borne chlamydospores of var. *acridiorum* probably serve to distribute the fungus within and between host populations. Periods of high humidity, which are irregular and relatively rare events in habitat such as the Sahel region, would induce germination of the chlamydospores aggregations and formation of the anamorph. Dispersal from these primary foci is probably by rain-splash. However, if these primary conidia fail to reach their insect target then an additional strategy, that of secondary conidiation through the formation of capilloconidia (Evans 1994), is also employed. Infection of nymphs must occur as they

come into contact with the sticky, mucus-covered spores during feeding and migration, whilst adults may be infected as they mate and oviposit in the soil.

Evans (1988) speculated that 'Many of the [entomopathogenic] *Ascomycotina* that made the transition from buffered tropical forest habitats to more seasonal, less predictable situations, appear to have sacrificed their teleomorph ... at an early stage in exchange for the massive production of dry conidia. This may be correlated with seasonal population explosions of the host insects, the fungus surviving in the soil during periods of low host density or unfavourable climatic conditions'. Undoubtedly, the trigger for *Syngliocladium acridiorum* was desertification in Africa as the host-pathogen association adapted to much drier habitats. Significantly, *Cordyceps* spp. were not recorded during comprehensive surveys for fungal pathogens of grasshoppers and locusts in Africa and the Near East (Shah *et al.* 1997). In contrast, however, they are not uncommon on these hosts in moist forest habitats, at least in the neotropics (Evans 1982).

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