INTRODUCTION

The arthroconidial genus Arthrophigis was proposed by Cochet (1939) with A. langeronii as the type species, but it was invalid because it lacked a Latin diagnosis, which was at that time still required as prerequisite by the International Code of Botanical Nomenclature. Sigler & Carmichael (1976) subsequently validated the genus name based on Odiodendron kalrae. In addition to the type species, A. kalrae, the genus currently includes three other taxa, A. alba, A. lignicola and A. pinicola (Sigler & Carmichael 1976, 1983, Sigler et al. 1990, Gené et al. 1996). Other species previously included in the genus were A. cuboidea and A. sulphurea. While the former species was transferred to the genus Scytalidum (Kang et al. 2010), A. sulphurea was considered a possible synonym of Pachysolen tannophilus (Saccharomyces) (von Arx 1985).

Apart from A. kalrae, which was traditionally associated with the sexual morph Eremomyces langeronii, other ascomycetes have been described with unnamed Arthrophigis morphs, i.e., Leucothecium coprophilum, L. emdenii and Faurelina indica (von Arx & Samson 1973, von Arx 1978, von Arx et al. 1981, Malloch & Sigler 1988, Valldosera et al. 1991). Arthrophigis species have been isolated from air, compost, marine sediments, soil, wood and, occasionally, from opportunistic infections in humans (de Hoog et al. 2011). Morphologically, they are recognised by a slow growth rate and by the presence of 1-celled, hyaline, smooth-walled, cylindrical arthroconidia released schizolytically from dendritic conidiophores (Sigler & Carmichael 1976). A particular feature of A. kalrae is the presence of a trichosporiella-like synasexual morph characterised by solitary, globose to subglobose conidia, which grow laterally and sessile on undifferentiated vegetative hyphae (Sigler & Carmichael 1983). Recently, a phylogenetic study based on sequences analysis of SSU, ITS and RPB2, revealed the polyphyly of Arthrophigis (Kang et al. 2010).

Another arthroconidial genus morphologically similar to Arthrophigis is Arthropilus. The genus comprises four species, i.e., Arthropilus cirhata, A. hispanica, A. microspora and A. truncata (Sigler et al. 1982, Sigler & Carmichael 1983, van Oorschot & de Hoog 1984, Ulfig et al. 1995). These fungi are usually reported from plant material, but A. hispanica, which was only known from marine sediments, has recently been isolated from clinical specimens (Giraldo et al. 2013). Arthropilus shows pigmented or non-pigmented arthroconidia, joined by adjacent connectives, released rheologically from undifferentiated conidiophores and occasionally has a Hunicola synasexual morph (Sigler et al. 1982, van Oorschot & de Hoog 1984). Van Oorschot & de Hoog (1984) questioned the distinction between Arthrophigis and Arthropilus, and suggested transferring Arthropilus species, excluding the type species A. kalrae, to the genus Arthropilus. Other authors, however, rejected this proposal (Malloch & Sigler 1988, Sigler et al. 1990).

In the present study we compared the D1/D2 sequences of the available types of Arthrophigis and Arthropilus spp. with those of taxa retrieved from GenBank to clarify their taxonomy, and to determine their phylogenetic relationships. By combining morphological observations with multilocus DNA sequence
analysis, several novel cryptic species of Arthrographis were delineated, which are newly described in this study.

MATERIALS AND METHODS

Isolates

The fungal isolates and DNA sequences included in the study are shown in Table 1. Twenty-six clinical Arthrographis isolates were provided by the Fungus Testing Laboratory at the University of Texas Health Science Center (UTHSC), the majority previously identified as A. kairaee by Giraldo et al. (2013). Because these isolates varied in morphology and their DNA sequence data, all isolates were re-examined in the present study. The type strains from the new species described here were deposited in the CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands.

Phenotypic studies

Isolates were studied following the criteria of Sigler & Carmichael (1976, 1983) and Ullig et al. (1995). Morphological features were examined on potato dextrose agar (PDA; Pronadisa, Madrid, Spain), 2 % malt extract agar (MEA; BD Difco™ Franklin Lakes, N.J., USA), potato carrot agar (PCA; potatoes, 20 g; carrot, 20 g; agar, 20 g; distilled water to final volume of 1 000 mL) and oatmeal agar (OA; filtered oat flakes after 1 h of simmering, 30 g; agar, 20 g; distilled water to final volume of 1 000 mL). Cultures were incubated at 25 °C in the dark for 4 wk. Colony diameters were measured after 14 d of incubation and rated according to the colour charts of Kornepur & Wanscher (1978). Microscopic features were examined and measured in either 85 % lactic acid or lactophenol cotton blue under a light microscope Olympus CH-2 (Olympus Corporation, Tokyo, Japan). Photomicrographs were obtained with a Zeiss Axio-Imager M1 light microscope (Zeiss, Oberkochen, Germany), using phase contrast and Nomarski differential interference.

The ability of the fungi to grow at 15, 20, 25, 30, 35, 37, 40, 42 and 45 °C was determined on PDA. To determine the resistance to cycloheximide, isolates were transferred to Petri dishes containing PCA supplemented with chloramphenicol (200 mg/L) and cycloheximide at a final concentration of 2 g/L, and incubated at 25 °C for 2 wk. All tests were performed in duplicate. To evaluate the ability of isolates to convert to the yeast phase, a portion from a fresh culture on PDA was transferred to tubes with Brain Heart Infusion broth (BHI; Becton Dickinson & Company, Franklin Lakes, N.J., USA) and incubated at 37 °C for 2 wk. Subsequently, several transfers to BHI broth were performed.

DNA extraction, amplification and sequencing

Isolates were grown on yeast extract sucrose agar (YES; yeast extract, 20 g; sucrose, 150 g; agar, 20 g; distilled water to final volume of 1 000 mL) for 10 d at 25 °C and DNA extracted using PrepMan Ultra sample preparation reagent (Applied Biosystems, Foster City, CA, USA), according to the manufacturer’s protocol. The DNA was quantified using NanoDrop 3000 (ThermoScientific, Ashevile, NC, USA). The internal transcribed spacer (ITS) regions and D1/D2 domains of the 28S rDNA were amplified with the primer pairs ITS5/ITS4, NL1/NL4b and LR0R/LR5 (Vilgalys & Hester 1990, White et al. 1990, O’Donnell 1993). A portion of the actin gene (ACT1) was amplified using the primer set Act1/Act4 (Voigt & Wöstemeyer 2000) and a chitin synthase gene (CHS1) using the primers CHS-79F/CHS-354R (Carbone & Kohn 1999). PCR products were purified and sequenced at Macrogen Europe (Amsterdam, The Netherlands). The program SeqMan v. 7.0.0 (DNASTAR, Madison, WI, USA) was used to obtain consensus sequences of each isolate. In addition, numerous D1/D2 sequences, corresponding to different classes, orders and families of ascomycetes retrieved from GenBank or NITE/NRBC databases were included in the phylogenetic study (Table 1). Most of these sequences were published by different authors (Sugiyama et al. 1999, Sugiyama & Mikawa 2001, Untereiner et al. 2002, Reeb et al. 2004, Xi et al. 2004, Murata et al. 2005, Wang et al. 2005, Wedin et al. 2005, Kodseu et al. 2006, Réblová & Seifert 2007, Tsui et al. 2007, Gueidan et al. 2008, Boehm et al. 2009, Sugiyama et al. 2002, Boonmee et al. 2011, Pettersson et al. 2011, Réblová et al. 2011, Giraldo et al. 2013). The selection of these sequences was based on the results of a BLAST search using the D1/D2 and ITS sequences from each of the ex-type strains of the different species of Arthrographis and Arthropdis.

Phylogenetic analysis

Sequences were aligned using Clustal X v. 1.8 (Thompson et al. 1997) with default parameters, followed by manual adjustments with a text editor. The phylogenetic relationship between Arthrographis and Arthropdis species with other genera was determined through the analysis of D1/D2 sequences. Since genetic and also morphological variability was detected among isolates of Arthrographis, a multi-focus sequence analysis was carried out to confirm the results obtained from D1/D2 data. This analysis included a fragment of the ACT1 gene, the CHS1 gene and the ITS region. Phylogenetic analyses were performed with MEGA v. 5.05 (Tamura et al. 2011), using the Maximum Composite Likelihood (ML). The selection of the best nucleotide substitution model (Tamura-Nei with Gamma distribution) was made using the model selection analysis under MEGA v. 5.05. Gaps or missing data were treated as partial deletion with a site coverage cut-off of 95 % and Nearest-Neighbour-Interchange (NNI) used as Heuristic method. The internal branch support was assessed by a search of 1 000 bootstrapped sets of data. DNA sequence data were deposited in GenBank (Table 1), the alignment and trees in TreeBASE (http://www.treebase.org) and taxonomic novelties in MycoBank (http://www.MycoBank.org; Crous et al. 2004).

RESULTS

Phylogenetic analyses

The D1/D2 phylogenetic tree that included the ex-type strains of the different species of Arthrographis and Arthropdis and representative members of different fungal classes and orders revealed that both genera are polyphyletic (Fig. 1). The type species of Arthrographis, A. kairaee, was included in a well-supported clade within the Dothideomycetes (85 % bootstrap, bs), forming together a highly supported subclade (99 % bs) with Rhexothecium globosum, Eremomycyes bilateralis, E. fangeroni and four unidentified species of Arthrographis. While the ex-type strain of Arthrographis lignicola was related to different genera of the Lecanoromycetes, such as Sarea and Pycnora, the ex-type strains of Arthrographis pinicola and A. alba were associated with the Eurotomyces (99 % bs). Arthrographis pinicola and Eremascus albus (Eremascaleaceae) formed a well-supported clade (93 % bs), while A. alba and Leucothecium emdenii formed a well-supported clade (99 % bs) within the Onygenales.

The type species of Arthropdis, A. truncata, clustered with Poro­sphaerella borinquensis and Coniochaeta velutina (99 % bs), both members of Sordariomycetes. Arthropdis cirrhata and A. hispanica were accommodated within the Onygenales. The only available reference strain of A. microsperma grouped with different members of the Helotiales (94 % bs).

The multilocus sequence analysis was carried out with the ex-type strains of Arthrographis kairaee (CBS 693.77) and Ere­momycyes langeronii (CBS 203.78), 12 isolates identified as A. kairaee and five isolates identified as an Arthrographis sp. Due
| Species | Strains included in this study. |
|---------|--------------------------------|
| Acarospora smaragdula | – Unknown, Sweden |
| Ajellomyces dermatitidis | – ATCC 18187, Human, unknown |
| Amauroascus albicans | – NRRL 5141, Soil, Honduras |
| Apinisia graminicola | – CBS 156.77, Skin lesion in dog, USA |
| Aquaphila albicans | – BCC 3520, On wooden test block (Acacia oblonga), Thailand |
| Arachnomyces minimus | – CBS 324.70, Decayed wood, Canada |
| Arachnotheca glomerata | – CBS 348.71, Unknown, Central African Republic |
| Arthroderma cajetanum | – UAMH 2937, Single ascospore isolate from a gymnothecium on soil, unknown |
| Arthroderma ciferrii | – CBS 272.66, Soil, USA |
| Arthroderma ciferrii | – CBS 272.66, Soil, USA |
| Arthrographis alba | – CBS 370.92, Marine sediments, Spain |
| Arthrographis arxii | – CBS 203.78, Dung of herbivore, India |
| Arthrographis chlamydospora | – UTHSC 06-1053, Urine, USA |
| Arthrographis curvata | – FMR 4032, Marine sediments, Spain |
| Arthrographis globosa | – UTHSC 11-757, Marine sediments, Spain |
| Arthrographis globosa | – UTHSC 06-1053, Urine, USA |
| Arthrographis kalrae | – CBS 693.77, Sputum, India |
| Arthrographis lignicola | – CBS 689.83, Gymnosperm wood chips and bark, Canada |
| Arthrographis longispora | – UTHSC 05-1203, Marine sediments, Spain |
| Arthrographis pinicola | – CBS 653.89, Gallery of Ips latidens in Pinus contorta, Canada |
| Arthropsis cirrhata | – CBS 628.83, Wall, The Netherlands |
| Arthropsis hispanica | – CBS 351.92, Bottom of water deposit, Spain |
| Arthropsis hispanica | – CBS 351.92, Bottom of water deposit, Spain |

Table 1 Strains included in this study.
| Species                        | Collection | Location                  | Accession Number(s) | Notes |
|-------------------------------|------------|---------------------------|---------------------|-------|
| Arthropsis microsperma        | UAMH 4290  | Grass, England             | HG00451             |       |
| Arthropsis truncata           | CBS 584.82 | Leaf litter, Perú          | HG00450             |       |
| Chalas longipes               | NBRC 100564| Decaying fir needles, Japan|                     |       |
| Chlamydotubellia huakangpangelsis | UAMH 10912| Ex gametophytes of Hylcomium splendens, Canada | JN85198             |       |
| Ctenomyces serratus           | CBS 187.61 | Soil, Australia            | AB040683            |       |
| Eremascus albus               |            |                           | FJ53823             |       |
| Eremomyces bilaterralis       | CBS 781.70 | Dung of pack rat, USA      | HG004545            | HG316562 |
| Eurotium herbariorum          | CBS 516.65 | Unpainted board, USA       | JF922029            |       |
| Faurella indica               | CBS 126.78 | Dung of cow, India         | GU160864            |       |
| Geomyces pannorum             | UAMH 10473 | Ex biofilm on soil, United Kingdom | GU160866            |       |
| Gymnoascus reesii             | CBS 795.70 | Soil, USA                  | FJ922021            |       |
| Malbranchea aurantiaca        | CBS 655.71 | Clay soil, USA             | AB040684            |       |
| Malbranchea cinnamomea        | CBS 548.72 | Dung of Guinea pig, India  | AB040687            |       |
| Mallochia reticulata          | CBS 392.61 | Rhizosphere of Musa sapientum, Honduras | AB075320            |       |
| Monascus lunisporas           | CBS 113675 | Soil, Brazil               | JF922026            |       |
| Monascus ruber                | CBS 242.34 | Unknown, Canada            | FJ922025            |       |
| Onygena corvina               | JCM 9546   | Decaying bone, Japan       | AB075355            |       |
| Onygena equina                | CBS 947.70 | Cow hoof, Germany          | AB075356            |       |
| Osteichnium curtisii          | CBS 198.34 | On Quercus sp., USA        | FJ61186             |       |
| Polytricha aurantiaca         | CBS 990.72 | Unknown, France            | FJ922020            |       |
| Porosphaerella borinqueinensis| ICMP 15117 | Wood, New Zealand          | EF063573            |       |
| Pseudoaerocochlitos trochochapos | CBS 559.71 | Soil, USA                  | AB075344            |       |
| Pyromyces xanthococcacca      |            | Urqueni, Sweden            | AV53388             |       |
| Rhexothecium globosum         | CBS 955.73 | Desert soil, Egypt         | HG004544            |       |
| Rutstroemia curvisi          | NBRC 9671  | Dung of rabbit, England    |                     |       |
| Rutstroemia paludosa          | NBRC 9672  | On Syplocarpus foetidus, USA|                     |       |
| Sarcocleotia globosa          |            |                           | SY89409             |       |
| Sarcolaresina                 |            |                           | SY64096             |       |
| Scleromitrula shiraiana       | NBRC 30255 | On Morus bombycis, unknown | Scleromitrula shiraiana |       |
| Scytalidium cuboideum         | UAMH 7144  | Ex Lingula specimen, USA   | AB213427            |       |
| Scytalidium cuboideum         | UAMH 9435  | Bronchial washing, USA     | AB213428            |       |
| Shanorella spirotricha        | CBS 304.86 | Dung of rabbit, USA        | FJ538288            |       |
| Stromatina gladii             | NBRC 7169  |                           |                     |       |
| Trichophyton ajelloi var. ajelloi | NBRC 7169 |                           | AB075329            |       |

1. ATCC: American Type Culture Collection, Manassas, VA, USA; BCC: Biotechnology Culture Collection, National Center for Genetic Engineering and Biotechnology (BIOTEC), Bangkok, Thailand; CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; FRR: culture collection of CSIRO, Australia; FMR: Faculty of Medicine Reus, Spain; HKUCC, Hong Kong University Culture Collection, Department of Ecology and Biodiversity, Hong Kong, China; ICMP: International Collection of Microorganisms, Landcare Research, Auckland, New Zealand; JCM: Japanese collection of microorganisms; NBRC: NITE Biological Resource Center, Japan; UAMH: University of Alberta Microfungus Collection and Herbarium; EDMONTON, CANADA; UTHSC: Fungus Testing Laboratory, University of Texas Health Science Center, San Antonio, TX, USA; 1 = Ex-type strain.
2. Accession numbers of sequences newly determined in this study are indicated in bold.
3. ITS: internal transcribed spacer regions of the nrDNA and intervening 5.8S nrDNA; ACT1: partial actin gene; CHS1: chitin synthase gene.
Fig. 1 Maximum-likelihood (ML) tree constructed with sequences of the D1/D2 domains of the 28S rRNA gene. Bootstrap support values above 70 % are indicated at the nodes. The phylogenetic tree was rooted to Peziza varia and Peziza phyllogena. \( ^\text{T} \) = Ex-type strain.
to the low intra-specific variability detected in the ITS sequences among the 22 isolates identified as A. kalaiae (98.5–100 % similarity), we selected 12 isolates that represented the most characteristic morphological variants observed.

With the primers used, we were able to amplify and sequence 300–350 bp, 450–500 bp and 750–820 bp of the CHSt gene, the ITS region and ACT1 gene, respectively. The topology of the combined ML tree was similar to trees based on individual genes (data not shown). The combined tree included 1 544 bp and showed four main lineages (Fig. 2). The largest lineage was represented by a clade with 12 clinical strains of A. kalaiae, including the ex-type strain. Sequences within the clade were practically identical, showing similarities of 98.5–100 % for each over the three loci. The second lineage (Arthrographis sp. I, 100 % bs) included one strain from marine sediments (FMR 4032) and another from nails (UTHSC 11-1163), with an intra-specific similarity of 99–100 %. The third lineage (Arthrographis sp. II) comprised only one strain (UTHSC 05-3220) from clinical origin (foot). Finally, the fourth lineage comprised a clade with three strains separated from each other by a considerable genetic distance. They were the clinical strains UTHSC 06-1053 (Arthrographis sp. III) and UTHSC 11-757 (Arthrographis sp. IV) and CBS 203.78, the ex-type strain of E. langeronii from herbivore dung. The latter two strains formed a well-supported subclade and showed genetic similarities that ranged from 93.8 % for ITS region to 96–96.7 % for CHSt and ACT1 genes. Surprisingly, the ex-type strains of A. kalaiae and E. langeronii were located in two different clades, showing genetic similarities of 94.1 % for ITS region and 92.8 % and 88.1 % for ACT1 and CHSt genes, respectively.

**Phenotypic studies**

Most of the strains included in the A. kalaiae clade (Fig. 2) showed the typical morphotypic characters described for the species; i.e., colonies at 25 °C with slow to moderate growth (up to 10–21 mm diam after 10 d on PDA), flat to slightly folded, initially beige and moist with a yeast-like appearance, becoming tan or yellowish and powdery to granular (Fig. 3a–f); conidiophores hyaline and usually branched (Fig. 3g); conidigenous hyphae hyaline, simple or branched; arthroconidia 1-celled, hyaline, smooth-walled, cylindrical with truncate ends, 2.5–9 × 1–2 μm. All strains formed a trichosporiella-like synasexual morph with sessile, globose to subglobose, hyaline, thin and smooth-walled conidia, 2–4 × 2–3 μm (Fig. 3h). Several strains showed some atypical characters not previously described for this species. The strains UTHSC 02-1022, UTHSC 06-982, UTHSC 07-2450, UTHSC 08-1804, UTHSC 08-2107, UTHSC 10-1652, UTHSC 10-2583 and UTHSC 11-1256 produced intercalary or terminal chlamydospores with smooth or slightly rugose walls. While in most of these isolates the chlamydospores were hyaline to subhyaline, those of strain UTHSC 11-1256 turned brown on PDA and OA (Fig. 3i, j) giving a dark pigmentation to the colony. The UTHSC 05-17 strain showed a predominance of small conidiophores (up to 70 μm long) composed of a terminal whorl of numerous short chains of clavate or cylindrical arthroconidia with rounded ends (Fig. 3k, l); in old cultures (12 wk) this isolate developed immature ascomata submerged in the agar of all media tested. These ascomata were spheroidal, non-ostiolate, 37–70 μm diam, with a dark brown, pseudoparenchymatous peridium of textura angularis, surrounded by brown hyphae (Fig. 3m).

*Arthrographis* sp. I (FMR 4032 and UTHSC 11-1163) (Fig. 5a–j) showed similar morphological characteristics to those of the A. kalaiae clade, but differed in the following features: the colonies on MEA 2 % were orange-yellow (4BB) and showed a very slow growth (6–7 mm diam in 14 d) (Fig. 5a); in addition to the trichosporiella-like synasexual morph (Fig. 5e), both strains produced on PDA at 25 °C and BHI at 37 °C curved and cashew-nut-shaped sessile conidia formed laterally on undifferentiated hyphae (Fig. 5f, g); and the strain UTHSC 11-1163 produced superficial spherical ascocoma with evanescent ascii and navicular ascospores (Fig. 5h–j).

The lineage representing *Arthrographis* sp. II (UTHSC 05-3220), produced membranous colonies in all the media tested (Fig. 7a, b),
conidiophores poorly differentiated (Fig. 7c, d) and arthroconidia longer (5–10(–13) µm) than those of the members of A. kalrae clade (Fig. 7e, f). In this strain, as in Arthrographis sp. III and Arthrographis sp. IV, the production of a trichosporiella-like synasexual morph was not observed.

Arthrographis sp. III displayed umbonate, cerebriform and velvety colonies on PDA (Fig. 4a), branched conidiophores (Fig. 4c, d), cylindrical, cubic and doliform arthroconidia (Fig. 4e–g) and terminal or intercalary globose chlamydospores (Fig. 4h).

Finally, the most representative morphological characters observed in Arthrographis sp. IV were the production of membranous colonies (Fig. 6a, b), poorly differentiated conidiophores (Fig. 6c) and doliform, ellipsoidal, slightly fusiform or globose arthroconidia (Fig. 6d, e).

All strains grouped in the clade of A. kalrae were able to grow at all the temperatures tested, attaining up to 30 mm diam at 40 °C and 5–15 mm at 45 °C on PDA after 14 d. Arthrographis sp. I and Arthrographis sp. III grew well at 37 °C (13–16 mm diam after 14 d), but at 40 °C the growth of both species was restricted (6–7 mm diam after 14 d). Conversely, Arthrographis sp. II and sp. IV were not able to grow at 37 °C. All isolates tolerated high doses of cycloheximide (2 g/L). Only isolates of A. kalrae were able to convert to a yeast phase, producing oval to ellipsoidal (2.5 × 4 µm) yeast-like budding cells at 37 °C after several transfers in BHI broth.

**Taxonomy**

On the basis of the morphological features observed, which correlated with the phylogenetic analysis, we concluded that Arthrographis spp. I–IV are different from the taxa currently accepted in this genus and are therefore described here as new. These species are named A. chlamydospora, A. curvata, A. globosa and A. longispora. In addition, the new name Arthrographis arxii is proposed for the ascomycete Eremomyces langeronii.
**Arthrographis arxii** Guarro, Giraldo, Gené & Cano, nom. nov.

— MycoBank MB804634

*Basionym. Pithoascus langeronii* Arx, Persoonia 10: 24. 1978.

≡ *Pithoascina langeronii* (Arx) Valmaseda, T.A. Martínez & Barrasa, Canad. J. Bot. 65: 1805. 1987.

≡ *Eremomyces langeronii* (Arx) Malloch & Sigler, Canad. J. Bot. 66: 1931. 1988.

*Etymology.* The specific epithet is given in honour of the mycologist Josef Adolf von Arx (1922–1988), who actively published on this group of fungi.

*Notes.* — Since our results demonstrated that *A. kalrae* and *E. langeronii* are not conspecific, and the name *A. langeronii* was occupied, a new name is proposed for *E. langeronii*.

**Arthrographis chlamydospora** Giraldo, Deanna A. Sutton, Gené & Madrid, sp. nov. — MycoBank MB804632; Fig. 4

*Etymology.* Referring to the presence of chlamydospores.

*Colonies on PDA at 25 °C attaining 15–16 mm diam after 14 d, pale to greyish orange (5A–B3) with whitish margin, umbonate, cerebriform, velvety. On OA and PCA at 25 °C attaining 23–25 mm and 15–16 mm diam, respectively, after 14 d, orange-white (5A2), flat, powdery or granulose. On MEA 2 % at 25 °C attaining 14–15 mm diam in 14 d, orange-yellow (4B8), flat, radially striated, granulose. At 37 °C on PDA the colonies attaining 12–13 mm diam after 14 d, brownish orange (6C3–4), cerebriform, velvety. *Vegetative hyphae* septate, hyaline, smooth- and thin-walled, 1.5–2 μm wide. *Conidiophores* mostly repeatedly branched, erect, up to 350 μm long, hyaline, smooth-walled. *Conidiogenous hyphae* simple or laterally branched, 1.5–2.5 μm wide, thick-walled, forming septa basipetally to form arthroconidia released via schizolytic secession. *Arthroconidia* unicellular, cylindrical, cuboid or doliiform, straight, 3–6(–7) × 1.5–2.5 μm, hyaline to subhyaline, thick- and smooth-walled. *Chlamydospores* terminal or intercalary, solitary, unicellular, globose or subglobose, 5–6 × 5–6 μm, hyaline, rough- and thick-walled, strongly chromophilic. Sexual morph and trichosporiella-like synasexual morph not observed.

Cardinal temperature for growth — Optimum 25–30 °C, maximum 42 °C, minimum 15 °C. The fungus was unable to grow at 45 °C.

*Specimen examined.* USA, Florida, from human urine, D.A. Sutton (holotype CBS H-21346, cultures ex-type CBS 135396, FMR 12129, UTHSC 06-1053).

**Arthrographis curvata** Giraldo, Gené, Deanna A. Sutton & Cano, sp. nov. — MycoBank MB804630; Fig. 5

*Etymology.* Referring to the presence of curved conidia.

*Colonies on PDA at 25 °C attaining 17–19 mm diam in 14 d, pale to greyish orange (5A–B3) with whitish margin, umbonate at centre and flat toward the periphery, powdery. On OA and
PCA at 25 °C attaining 19–20 mm and 24–26 mm diam, respectively, after 14 d, whitish, flat, dusty. On MEA 2% at 25 °C attaining 6–7 mm diam in 14 d, orange-yellow (4B8), elevated, cerebriform, membranous. At 37 °C on PDA the colonies attaining 15–16 mm diam after 14 d, orange-grey (5B2), flat, powdery. Vegetative hyphae septate, hyaline, smooth- and thin-walled, 1.5–2 µm wide. Ascomata cleistothecial, superficial, spherical, brown, 52–132 µm diam, peridium pseudoparenchymatous with textura angularis, surrounded by dark brown, thick-walled hyphae. Asci evanescent, globose, thin-walled. Ascospores unicellular, navicular in lateral view, ellipsoidal in front view, thin- and smooth-walled, without germ pores, 2.8–3.8 × 1.4–2 µm, hyaline to pale brown in mass. Conidiophores poorly differentiated, erect, simple or slightly branched, up to 35 µm long, hyaline, smooth-walled. Conidiogenous hyphae simple or branched, 1–2 µm wide, thin-walled, forming septa basipetally to form arthroconidia released by schizolytic secession. Arthroconidia unicellular, cylindrical or short-cylindrical, straight or slightly curved, 3–4.5(–7) × 1–2 µm, hyaline to subhyaline, thin- and smooth-walled. Synasexual morph trichosporiella-like with conidia growing directly on undifferentiated hyphae, lateral, sessile, globose, 2–3 µm diam, hyaline and smooth-walled. On PDA and BHI at 25 °C and 37 °C, respectively, conidia were occasionally observed to be unicellular, curved, cashew-nut-shaped, hyaline and smooth-walled, 3.5–6 × 1.5–2 µm, growing solitary and sessile on vegetative hyphae.

Cardinal temperature for growth — Optimum 25–30 °C, maximum 42 °C, minimum 15 °C. The fungus was unable to grow at 45 °C.

Specimens examined. Spain, Amposta, Ebro river, from river bank, K. Ullig (CBS 135934, FMR 4032). — USA, Colorado, from human nails, D.A. Sutton (holotype CBS H-21344, cultures ex-type CBS 135933, FMR 12125, UTHSC 11-1163).

Notes — The GenBank sequences AB128973.1 (ITS region) and AB128975 (28S rDNA), corresponding to the isolate E. langeronii UAMH 7600 from a fingernail, were 99.6 and 100 % (ITS region and 28S rDNA, respectively) similar to those of the type species of A. curvata.

Arthrographis globosa Giraldo, Deanna A. Sutton, Cano & Guarro, sp. nov. — MycoBank MB804633; Fig. 6

Etymology. Referring to the presence of globose conidia.

Colonies on PDA at 25 °C attaining 22–24 mm diam after 14 d, buttercup yellow (4A7), flat, membranous. On OA and PCA at 25 °C attaining 14–15 mm diam after 14 d, whitish, flat, at first glabrous becoming slightly powdery. On MEA 2% at 25 °C attaining 4–5 mm diam in 14 d, orange-yellow (4A8), cerebriform, membranous. Vegetative hyphae septate, hyaline, with golden pigment accumulation inside, smooth- and thin-walled, 1.5 µm wide. Conidiophores absent or poorly differentiated, hyaline, smooth-walled. Conidiogenous hyphae simple or branched, 1–1.5 µm wide, thin-walled, forming septa basipetally to form arthroconidia released via schizolytic secession. Arthroconidia unicellular, doliiform, ellipsoid, slightly fusiform or globose, 3–(5–)6.5 × 2–4 µm, hyaline, thick- and smooth-walled. Sexual morph, trichosporiella-like synasexual morph and chlamydospores not observed.
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Cardinal temperature for growth — Optimum 25–30 °C, maximum 35 °C, minimum 15 °C. The fungus was unable to grow at 37 °C.

Specimen examined. USA, Texas, from human bronchial wash, D.A. Sutton (holotype CBS H-21347, cultures ex-type CBS 135397, FMR 12124, UTHSC 11-757).

**Arthrographis longispora** Giraldo, Deanna A. Sutton, Cano & Guarro, sp. nov. — MycoBank MB804631; Fig. 7

*Etymology.* Referring to the length of the arthroconidia.

Colonies on PDA at 25 °C attaining 18–21 mm diam after 14 d, yellowish orange (4A7), radially folded or rugose at centre and flat toward the periphery, membranous. On OA and PCA at 25 °C attaining 18–21 mm and 8–9 mm diam, respectively, after 14 d, whitish, flat, at first glabrous becoming slightly powdery. On MEA 2 % at 25 °C attaining 11–12 mm diam in 14 d, orange-yellow (4B8), cerebriform at centre and flat toward the periphery, membranous. *Vegetative hyphae* septate, hyaline, with golden pigment accumulation inside, smooth- and thin-walled, 1.5–2 µm wide. *Conidiophores* poorly differentiated, erect, up to 60 µm long, hyaline, smooth-walled. *Conidiogenous hyphae* simple, occasionally slightly branched, 1–1.5 µm wide, thin-walled, septating basipetally to form arthroconidia released by schizolytic secession. *Arthroconidia* unicellular, cylindrical with truncated or rounded ends, straight or slightly curved, 5–10(–13) × 1–1.5 µm, hyaline, thin- and smooth-walled. Sexual morph, trichosporiella-like synasexual morph and chlamydospores not observed.

Cardinal temperature for growth — Optimum 25–30 °C, maximum 35 °C, minimum 15 °C. The fungus was unable to grow at 37 °C.

Specimen examined. USA, Utah, from human foot, D.A. Sutton (holotype CBS H-21345, cultures ex-type CBS 135935, FMR 12101, UTHSC 05-3220).

**DISCUSSION**

The genus *Arthrographis* was traditionally considered a member of the *Eremomycetaceae*, *Dothideomycetes* (Malloch & Sigler 1988). However, our D1/D2 analysis demonstrated that only the type species, *A. kalrae*, and the new taxa proposed here (i.e., *A. arxii*, *A. chlamydospora*, *A. curvata*, *A. globosa* and *A. longispora*) are members of the family, and that the name *Arthrographis* should be restricted to these species. The other species previously attributed to the genus are phylogenetically distant from the type. *Arthrographis lignicola* belongs to the *Lecanoromycetes*, forming a weakly supported clade with *Sarea resinae*, *Pycnora xanthococca* and *Sarcoletia globosa*. Although a BLAST search using D1/D2 and ITS sequences of *A. lignicola* showed close relationships with other members of

**Fig. 6** *Arthrographis globosa* UTHSC 11-757. a, b. Colonies on PDA and MEA 2 %, respectively, after 21 d at 25 °C; c. poorly differentiated conidiophores; d. conidiogenous hyphae fragmenting schizolytically producing ellipsoidal, doliiform, slightly fusiform and globose arthroconidia; e. globose arthroconidia. — Scale bars = 10 µm.
that class, we could not include more sequences of Lecanoromycetes in our phylogenetic analysis due to the difficulties in performing a reliable alignment. *Arthrographis pinicola* and *A. alba* are accommodated in the Eurotiomycetes, more particularly, the former in Eremascaceae, closely related to *Eremascus albus*, and the latter in the Gymnoascaceae, closely related to *Leucothecium emdenii*. *Arthrographis alba* was described based on several isolates from different origins and, although some morphological similarity with the anamorph of *L. emdenii* was already mentioned, none of those isolates developed the sexual morph (Gené et al. 1996). The present study reveals that sequences from D1/D2 and ITS of both species are practically identical (data not shown), which indicates that *A. alba* must be considered the asexual morph of *L. emdenii*. The genus *Leucothecium* was described by von Arx & Samson (1973) to accommodate ascomycetes with yellowish globose ascomata, hyaline peridium, bivalve-lenticular ascospores and asexual morphs with hyaline arthroconidia. Currently, the genus comprises two species, *L. emdenii*, the type species, and *L. coprophilum*, both traditionally included in Gymnoascaceae on the basis of the morphology of the asexual morph and ascospores (von Arx & Samson 1973, Valldosera et al. 1991).

The ascomycete *Faurelina indica* also produces an arthrographis-like asexual morph similar to the *Arthrographis* anamorph of *E. langeronii* (von Arx 1978, von Arx et al. 1981). The genus *Faurelina*, with a coprophilous habitat, was originally included in the family Chadefaudiellaceae, Microascales (Locquin-Linard 1975, Cannon & Kirk 2007). This genus was characterised by pustulate or hemispherical ascomata, a peridium composed of vertical rows of dark cells, asci arranged in vertical chains and striate, and pale brown ascospores (Guarro et al. 2012). Our D1/D2 analysis revealed a well-supported relationship of *F. indica* with the Dothideomycetes, although distantly related to the genus *Arthrographis* and other members of Eremomycetaceae. Réblová et al. (2011), based on LSU sequences analysis, demonstrated the relationship of *F. indica* with the Didymellaceae, including it in the Pleosporales. The exclusion of *F. indica* from Microascales correlates with the morphological features of the asexual morph, since in that order the asexual morphs are characterised by percurrently proliferating conidigenous cells (annellides) usually belonging to the genera Scopulari-
 ops, Graphium, Scedosporium, Cephalotrichum and Wardomyces (Valmaseda et al. 1986, Zhang et al. 2006, Rébelová et al. 2011).

Eremomyces langeronii was traditionally considered to be the sexual morph of A. kalrae (von Arx 1978, Malloch & Sigler 1988). However, this connection was questioned by Sigler & Carmichael (1983), and later by Gené et al. (1996), arguing that both species produced different RFLP patterns. The present study confirms that E. langeronii and A. kalrae are not conspecific. Eremomyces langeronii was initially described as Pithoascus langeroni (von Arx 1978), later being transferred to the genus Pithoascina by Valmaseda et al. (1986). Malloch & Sigler (1988) accommodated this species in the genus Eremomyces (Eremomycestaceae) (Malloch & Cain 1971, Malloch & Sigler 1988) together with E. bilateralis and Rhexothecium globosum. Members of the Eremomycestaceae are characterised by cleistothecial ascocoma, clavate to ovoid, evanescent ascii, unicellular, hyaline to pale yellow-brown ascospores, arthropagnis-like or trichosporiella-like asexual morphs and a coprophilous habitat (Malloch & Sigler 1988). Similar morphological features such as non-ostiolate dark ascocoma and hyaline, unicellular ascospores can be also found in species of Pseudoeurotiales (incertae sedis, Lumbsch & Huhndorf 2010), but the members of this family display pale-brown or olive-brown ascospores at maturity and asexual morphs with poorly differentiated conidiophores sympodially producing subspherical to ovoidal conidia. Our study demonstrated that the family Eremomycestaceae encompasses the genera Arthropaghis s.str., Rhexothecium and Eremomyces (91.4–95.3 % intergeneric similarity in D1/D2 sequences). The latter now is restricted to E. bilateralis, which is the type species of the genus. Eremomyces bilateralis is distinguished from Arthropaghis s.str. and Rhexothecium by DNA sequence data (92.8 %, 89 % and 76.4 % similarity in D1/D2, ACT1 and ITS sequences, respectively) and by its cephalothecoid peridium, dark coloured colonies and the absence of an asexual morph (Malloch & Cain 1971).

The multilocus sequence analysis revealed the existence of four new species in Arthropaghis, A. curvata being the only one that showed both sexual and asexual morphs in culture. Its ascocoma and ascospores are similar to those of A. arxii; however, in A. arxii the ascocoma are immersed, and the ascocoma and ascospores are larger (75–160 µm diam and 2.7–5 × 1.8–2.6 µm, respectively). The asexual morph of A. curvata differs from A. arxii and A. kalrae mainly by less differentiated and poorly branched conidiophores, the presence of curved, sessile conidia and a restricted growth at 40 °C. Another fungus that also produces curved, cashew-nut shaped conidia is the type species of Arthropaghis s.lat. unable to grow at 37 °C are A. alba, A. lignicola and A. pinicola. Arthropaghis aiba produces white colonies, pseudodichotomously branched conidiophores and, in our study, this species was susceptible to high doses of cycloheximide (2 g/L). A. lignicola can be distinguished by its lemon-yellow to olive-green colonies with a diffusible brown pigment, narrow branched conidiophores and yellow arthroconidia; and A. pinicola produces floccose conidomata composed by repeatedly branched conidiophores and is susceptible to low doses of cycloheximide (Sigler & Carmichael 1983, Sigler et al. 1990, Gené et al. 1996).

In this study we observed some morphological variability in A. kalrae, with the presence of some characteristics not previously reported for this species. Such variations, however, did not correlate with genetic differences in any of the three loci sequenced. Several isolates showed chlamydospores that were terminal or intercalary, solitary or catenulate, hyaline or pigmented. In the protologue of Oidiodendron kalraii, based in the strain CBS 693.77, Tewari & Macpherson (1971) reported the occasional presence of oval to round, thick-walled chlamydospores; however, Sigler & Carmichael (1976) did not mention these structures and only reported the sessile conidia of the trichosporiella-like synasexual morph. The UTHSC 05-17 isolate produced infertile ascomata morphologically similar to the ascocoma produced by A. arxii and A. curvata, but in that isolate these structures were smaller (37–70 µm diam). That isolate also produced abundant conidiophores with whirls of short chains of clavate or cylindrical arthroconidia. The clavate conidia was reported by von Arx (1978) in the description of the asexual morph of E. langeronii, but probably this description was based on a single strain of this species and not on the ex-type strain of A. kalrae.

The genus Arthropaghis was established by Sigler et al. (1982) with A. truncata as the type species, to accommodate species with dark arthroconidia, joined by adjacent connectives and developed from undifferentiated conidigenous hyphae. Until now the species of this genus have not been associated to any sexual morph. Our D1/D2 sequence analysis demonstrates that Arthropaghis is polyphyletic and unrelated to Arthropaghis s.str. Arthropaghis hispanica and A. cirrata fall into the Onygenales, as do other species previously included in Arthropaghis. Other arthroconidial anamorphs of the Onygenales are included in the genus Malbranchea. However, Malbranchea is morphologically distinguished by its branched and arcuate fertile hyphae, straight in some species, that produce alternate arthroconidia (Sigler & Carmichael 1976). Our analysis placed the only available living strain of A. microsperma (UAMH 4290) in the Helotiales (Leotiomycetes). Arthropaghis microsperma was originally described by Berkeley & Broome (1873) as Oidium microspernum and later transferred to Arthropaghis by Sigler & Carmichael (1983) based on its arthroconidial ontogeny. Therefore, the name of this species should be reconsidered because Oidium anamorphs are currently associated with members of the Leotiomycetes (Braun & Cook 2012). Finally, Arthropaghis truncata is related to members of the Sordariomycetes. Although such type of asexual morphs have not been described in that class, humicola-like asporal morphs similar to the Humicola synasexual morph of A. truncata are present in some species of Chaetomium (Gené & Guarro 1996, Seifert et al. 2011). Further studies with a greater number of taxa of Sordariomycetes are needed to ascertain a defined position for A. truncata within this class.

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