## Isalonactis, a new genus of Roccellaceae (Arthoniales), from southern Madagascar

### Damien ERTZ, Anders TEHLER, Eberhard FISCHER, Dorothee KILLMANN, Tahina RAZAFINDRAHAJA and Emmanuël SÉRUSIAUX

**Abstract:** The new genus and species *Isalonactis madagascariensis* is characterized by a crustose, noncorticate, often sorediate thallus containing psoromic acid, tiny white pruinose ascomata with a thalline margin, an inconspicuous excipulum, a pale brown hypothecium, 3-septate hyaline ascospores and curved filiform conidia. Phylogenetic analyses using nuLSU and *RPB2* sequences place *Isalonactis* in the *Roccellaceae*, close to the genera *Lecanactis* and *Chiodecton*. The new species was collected on sheltered siliceous rocks in the dry landscape of the Isalo Massif (S Madagascar). *Dermatiscum thunbergii* is newly recorded from Madagascar.

Key words: Africa, Arthoniomycetes, desert, Lecanactis, lichen, phylogeny, taxonomy

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#### Introduction

Madagascar is a large island situated in the Indian Ocean at a minimum distance of 400 km from the African continent. It is well known for its remarkable biodiversity including many endemic taxa (Goodman & Benstead 2003). Despite the island being one of the most important biodiversity hotspots (Myers *et al.* 2000), its lichen flora remains very poorly studied with only 157 species included in the only available checklist (Aptroot 2013). This number contrasts with the 463 lichen taxa reported recently from

the neighbouring and much smaller island of Reunion (van den Boom et al. 2011). During a field trip in 2008, five of the authors (DE, EF, DK, TR and ES) were able to prospect several biomes, for example montane rainforests, dry forests, semideserts with rock outcrops, and detected numerous new records for the island. Most of these were widespread species not confined to Madagascar. However, the study of our material enabled us to describe the new lichen genus Savoronala Ertz et al., forming stipes producing sporodochia and thriving on Erica stumps and branches in heathlands in coastal sand dunes (Ertz et al. 2013). New lichen species were also discovered such as Syncesia madagascariensis Ertz et al., one of the few species of the genus having ascospores with more than three septa (Ertz et al. 2010), and Dirina madagascariensis Tehler et al., a cryptic species revealed by a detailed phylogenetic study of the genus (Tehler et al. 2013a). Further study of our material revealed a puzzling sorediate crustose member of the Roccellaceae collected in the semidesert landscape of the Isalo Massif. The aim of the present paper is to describe it and assess its phylogenetic position.

D. Ertz (corresponding author): Jardin Botanique National de Belgique, Département Bryophytes-Thallophytes, Domaine de Bouchout, B–1860 Meise, Belgium. Email: damien.ertz@br.fgov.be

A. Tehler: Naturhistoriska riksmuseet, Enheten för kryptogambotanik, Box 50007, S-104 05 Stockholm, Sweden.

E. Fischer and D. Killmann: Institute for Integrated Natural Sciences, Department of Biology, University of Koblenz-Landau, Universitätstraße 1, D-56070 Koblenz, Germany.

T. Razafindrahaja: Département Botanique, Parc de Tsimbazaza, B.P. 4096, Antananarivo 101, Madagascar. E. Sérusiaux: Evolution and Conservation Biology, University of Liège, Sart Tilman B22, B-4000 Liège, Belgium.

#### **Material and Methods**

Specimens were studied using an Olympus SZX12 stereomicroscope and an Olympus BX51 microscope. Hand-cut sections were investigated using light microscopy on material mounted in water and 5% KOH. Measurements of ascospores and conidia refer to material examined in water, those of asci to material examined in K/I. Ascospore measurements are indicated as (minimum)– $\bar{x}$  – SD –  $\bar{x}$  + SD (–maximum), where  $\bar{x}$  is the mean value and SD standard deviation, followed by the number of measurements (*n*). Chemical reactions were tested using KOH (K) and Lugol's reagent either without (I) or with (K/I) pre-treatment with K. Thinlayer chromatography (TLC) of acetone extracts was performed in solvent systems C and G (Orange *et al.* 2001).

We used DNA sequences from two loci, the nuclear large subunit ribosomal RNA gene (nuLSU), and the second largest RNA polymerase subunit (*RPB2*), of which six were newly produced for this study (Table 1). Other sequences were mainly sampled from a previously published larger dataset of *Arthoniales* including the family *Roccellaceae* (Ertz & Tehler 2011), with a few additional sequences from Tehler *et al.* (2013*b*). The two datasets were analyzed both separately and combined. Extractions, amplifications and sequencing procedures generally follow Ertz *et al.* (2009, 2011). Alignments were carried out with ClustalW (2.1) from within the program Mesquite v.2.75 (http://mesquiteproject.org).

For the phylogenetic analyses, we used the programs T.N.T. Tree Analysis Using New Technology 1.1 (Goloboff *et al.* 2008) and MrBayes 3 (Ronquist & Huelsenbeck 2003). In all analyses gaps were treated as missing data.

The parsimony analyses used the New Technology search with sectorial search, ratcheting, drifting, tree fusing and driven search options in effect, all using default settings. Resampling tree searches was done with parsimony jackknifing (Farris et al. 1996) under the New Tech search as implemented in T.N.T. (Goloboff et al. 2008); 1000 replicates submitted to TBR branch swapping were conducted. In parsimony jackknifing, the data are internally resampled with a jackknifing technique to find well-supported groups. Resampling works by calculating a tree for each of a large number of subsamples (pseudoreplicates) of characters from the data, then finding a summary tree, which comprises the groups occurring in the majority of the trees for subsamples. The tree for each pseudoreplicate is found by parsimony analysis, and each pseudoreplicate is formed by randomly selecting characters from the data without replacement, each character having a fixed chance 1/e (about 36%) of being excluded. With this resampling technique, the actual number of characters used may vary from replicate to replicate. Groups found in less than 50% of the trees for pseudoreplicates were discarded, thus eliminating unjustified (poorly supported) resolution caused by ambiguous datasets.

In the Bayesian inference analyses, the best model for nucleotide substitutions was selected for each locus individually by applying the Akaike Information Criterion (AIC; Akaike 1973) and the program MrModeltest 2.2 (Nylander 2005) in conjunction with PAUP\* (Swofford 1998). The selection of substitution models supported the GTR+I+ $\Gamma$  model for both partitions. Posterior probabilities of trees and parameters in the substitution models were approximated with MCMC and Metropolis coupling using the program MrBayes 3.2.1 (Ronquist & Huelsenbeck 2003). The Bayesian analyses were run for 10 million generations with two independent runs and four chains of Markov chain Monte Carlo (MCMC). The burn-in and convergence diagnostics were estimated using the PSRF (potential scale reduction factor), where values closer to 1 indicated convergence between runs (Gelman & Rubin 1992), and TRACER (Rambaut & Drummond 2007), making sure that the ESS values were higher than 200. The final majority-rule tree obtained from the Bayesian analyses is based on 17000 trees from the posterior of the two runs.

#### Results

Altogether we analyzed nuLSU rDNA and RPB2 sequences from two newly sequenced samples of *Isalonactis madagascariensis* (newly described below) and one newly sequenced sample of *Chiodecton leptosporum* Müll. Arg., together with 43 samples representing 40 other already phylogenetically analyzed species of *Roccellaceae*. In addition, three outgroup species were chosen among the *Opegraphaceae* (Ertz & Tehler 2011; Tehler *et al.* 2013*b*). Parsimony jackknife analysis showed that the individual gene trees were topologically similar, with no conflicts detected, although the nuLSU tree was more poorly resolved.

Since there were no conflicts in tree topology between the trees received from the Bayesian inference and the Parsimony jackknife analyses, we chose for the sake of simplicity to plot the Parsimony jackknife frequencies directly onto the Bayesian tree which was more highly resolved (Fig. 1). In the Bayesian tree, *Isalonactis* (newly described below) appears as a monophyletic group in a sister group relationship with the genus *Lecanactis*, and the next larger group includes the genus *Chiodecton* as sister group. In the Parsimony jackknife tree (not shown), these three genera were left unresolved in a trichotomy.

Species	Locality	Year	Collector	Collection no.	Genbank Acc. No.	
					nuLSU	RPB2
Austroroccella gayana	Chile, Los Lagos, Chiloe Prov., Ancud	2009	Anders Tehler	9852	KF036031	KF036042
A. gayana	Chile, Los Lagos, Bahia Mansa	2009	Anders Tehler	9855-3	KF036032	KF036043
Chiodecton natalense	Zambia, SE of Mbala	2004	Damien Ertz	6576	EU704085	EU704014
C. leptosporum	Reunion, Saint-Denis	2012	Damien Ertz	17886	KF831578	KF831579
Dendrographa decolorans	Spain, Mallorca, Cala Figuera	2007	Anders Tehler	9019	HQ454603	HQ454743
D. conformis	Mexico, Baja California, Ensenada, Pta Banda	2007	Anders Tehler	9083	HO454590	HO454730
D. leucophaea	Mexico, Baja California, Ensenada, Pta Banda	2007	Anders Tehler	9104	HO454522	HO454662
Dictvographa varians	Socotra, Sefflah	2008	Anders Tehler	9346	HO454576	HO454716
Dirina candida	Mallorca, Plava de Cala Santanví	2007	Anders Tehler	9004	KC108261	KC108065
D. catalinariae	Mexico, Baia California, Ensenada, Pta Banda	2007	Anders Tehler	9087	GU137909	GU137543
D. ceratoniae	Mallorca, Ses Covetes	2007	Anders Tehler	9047	FI638966	FI639025
D. massiliensis	Sweden, Gotland, Hoburgen	2007	Anders Tehler	9211	KC108356	KC108163
Enterographa crassa	France, Pas-de-Calais	2003	Damien Ertz	5041	EU704088	EU704020
E. hutchinsiae	Belgium, Bohan-Membre	2006	Damien Ertz	10066	EU704089	EU704021
Ervthrodecton granulatum	Gabon, Makokou	2006	Damien Ertz	9908	EU704090	EU704022
Isalonactis madagascariensis	Madagascar, Isalo Massif	2008	Damien Ertz et al.	13021	KF831576	KF831580
L madagascariensis	Madagascar, Isalo Massif	2008	Damien Ertz et al.	13024	KF831577	KF831581
Lecanactis abietina	Sweden, Uppland, Svartnö	2004	Anders Tehler	8550	EF081392	DO987635
L. horbonica	Reunion, sud de Saint-Denis/Le Brûlé	2003	Damien Ertz	4780	EU704092	EU704024
L. luteola	Chile, Antofagasta Prov., Cerro Moreno	2009	Anders Tehler	9926	HO454595	HO454735
Opegrapha milgata	Relgium, Roisin	2005	Damien Ertz	7564	EU704108	EU704044
Roccella fuciformis	Portugal, Estremadura, Cabo da Roca	2010	Anders Tehler	10200	KF036035	KF036046
R. gracilis	Peru, Dept. Pacasmavo, Cerro Chilco	2006	Anders Tehler	8892	FI638983	FI639042
R. montagnei	Kenva, Kilifi distr., Mida Creek	2007	Anders Tehler	9235-11	GU137967	GU137601
R phycopsis	France, Var. Isles d'Hyeres, Isle de Port-Cros	2008	Anders Tehler	9511	KF036036	KF036047
R tinctoria	Canary Islands, Tenerife, Buenavista del Norte	2000	Anders Tehler	8308	KF036037	KF036048
Roccellina accedens	Chile, Coquimbo Proy., Bahia Conchali.	2001	Anders Tehler	8451	EF081432	DO987675
R cerebriformis	Chile, Coquimbo Prov., 22 km N La Serena	2001	Anders Tehler	8386	HO454585	HO454725
R chalvhea	Chile, Valparaiso Prov. Los Molles, Punta Molles	2001	Anders Tehler	8355	HO454589	HO454729
R hypomecha	South Africa, Western Cape Prov. Vzerfontein	1996	Anders Tehler	7785	EE081438	DO987681
R inaequabilis	Chile, Coquimbo Proy, Parque Nacional Fray Jorge	2001	Anders Tehler	8368	EF081439	DO987682
R limitata	Chile, Coquimbo Prov., Guanaqueros	2001	Anders Tehler	8375	EF081440	DO987683
R mahujana	Chile Valparaiso Prov. Rocas de Santo Domingo	2001	Anders Tehler	8459	HO454596	HO454736
R mollis	Chile Coquimbo Prov. Tongov	2001	Anders Tehler	8372	FF081443	DO987686
R portentosa	Chile Valparaiso Prov. Los Molles Punta Molles	2001	Anders Tehler	8350	EF081446	DO987689
R terrestris	Chile Antofagasta Prov. Cerro Moreno	2001	Anders Tehler	9917	HO454598	HO454738
Schismatomma dirinellum	Spain Mallorca Ses Covetes	2007	Anders Tehler	9051	HQ454611	HQ454751
S divinellum	Spain, Andalucia, Cádiz distr. N of Barbate	2007	Anders Tehler	9815-10	KE036039	KE036050
S. annaum	Sweden Uppland Furgeund	2005	Anders Tehler	8551	EE081451	DO087604
Sigridea californica	Mexico Baja California Ensenada Pta Banda	2004	Anders Tehler	9095	HO454637	HO454777
S californica	Mexico, Baja California, Punta Banda	2007	Anders Tehler	9110	HQ454638	HQ454778
Sparria andlichari	Belgium Brûlv-de-Pesche vallée de l'Eau Noire	2007	Damian Erta	12651	HQ454511	HQ454652
Suncesia haguaijensis	USA Hawaii Hawaii North Kona Distr Kalaoa	2010	Anders Tehler	10156-27	KE036040	KF036051
S intercodons	Rwanda forêt de Nyungwe	2010	Damien Frtz	11059	HO454644	HO454784
S. madagascarionsis	Madagascar Ambalamanakana Ankazomiyady	2007	Damien Ertz	12966	HO454645	HO454785
S. myrticola	Portugal, Azores, Terceira, Quatro Ribeiras	2008	Anders Tehler	10252	KF036041	KF036052

TABLE 1. Specimens used in phylogenetic analyses of the Arthoniales. GenBank accession numbers in bold are new sequences from this study.

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FIG. 1. Two-locus (nuLSU + RPB2) majority-rule tree received from Bayesian analysis showing the proposed phylogenetic relationships among 46 specimens representing 37 species of *Roccellaceae* with three species of *Opegraphaceae* (*Opegrapha vulgata, Dictyographa varians* and *Sparria endlicheri*) chosen as outgroups. Bayesian posterior probability values shown above nodes. Parsimony jackknife frequencies received from parsimony analyses were plotted below nodes (x = frequency below 50%). For readability, values and frequencies are shown for genera and larger groups only. Collecting numbers of the authors following the species names act as specimen and sequence identifiers. Species within single quotes are names for which we regard recombination in a more appropriate genus as premature and thus the old name is retained.

#### Isalonactis madagascariensis Ertz, Tehler, Eb. Fisch., Killmann, Razafin. & Sérus. gen. et sp. nov.

# MycoBank No.: MB807014 (genus) and MB807015 (species)

Taxon belonging to the *Roccellaceae* and characterized by the combination of the following characters: crustose, non-corticate, cracked to areolate thallus *c*. 0.2-0.7 mm thick containing psoromic acid, tiny ascomata having a thalline margin, a white pruinose hymenial disc, an inconspicuous excipulum and a pale brown hypothecium, 3-septate hyaline ascospores of (20.0-)22.5-27.0  $(-29.0) \times (4.5-)5.0-5.5(-6.0)$  µm, and curved to sickle-shaped filiform conidia.

Type: Madagascar, Isalo Massif near ANGAP house and National Park border, 851 m alt., 22°37'8·1"S, 45°21'42·6"E, Mesozoic sandstone cliffs with *Coleochloa* setifera, Ischnolepis tuberosa and Pachypodium gracilius, on sheltered rock, 7 October 2008, D. Ertz 13024, E. Fischer, D. Killmann, T. Razafindrahaja & E. Sérusiaux (BR—holotype; S—isotype).

(Fig. 2)

*Thallus* epilithic, thin, non-corticate, *c*. 0.2-0.7 mm thick, smooth, finely cracked to areolate, pale cream, matt; presence of numerous hyaline crystals 0.5-3.0 µm diam. covering the hyphae, dissolving in K (polarized light); *prothallus* absent or dark brown, up to 0.5 mm wide. *Photobiont Trentepohlia*; cells  $11-20 \times 8-12$  µm.

Ascomata apothecioid, circular to irregular in outline, sometimes with an undulated or folded margin, scattered, erumpent, semiimmersed to sessile, not or slightly constricted at the base, usually one per areole, (0.2-)0.3-0.5(-0.8) mm diam., with a thin non-corticate thalline margin of 50-70 µm thick, level with the hymenial disc, of the same colour as the thallus; hymenial disc exposed, pale brown, covered by a white pruina. Exciple inconspicuous. Hymenium 85–110 μm tall, hyaline, not inspersed with oil droplets, I+ red, K/I+ blue; epihymenium pale to dark reddish brown, K- (but reddish tinge disappearing); hypothecium 75-150 μm tall, pale to dark brown, I- (orange), K-(but reddish tinge disappearing). *Paraphysoids* sparsely branched in the hymenium, richly branched in the epihymenium, 2 µm thick, not or only slightly enlarged at apices; apices dark brown, 5–15 µm long. Asci clavate, 55–

 $65 \times 15-16$  μm, 8-spored, K/I– except for an amyloid (blue) endoascus layer in the upper part. Ascospores (20.0–)22.5–27.0 (-29.0) × (4.5–)5.0–5.5(-6.0) μm (n = 23), (2–)3-septate, septation starting with one median septum, not constricted at septa, cells more or less equal in size; gelatinous sheath absent (at ×1000).

*Pycnidia* immersed in the thallus, visible as pale to dark brown punctiform spots 40–70  $\mu$ m diam, *c*. 200 × 100  $\mu$ m; pycnidia wall very thin, hyaline to pale brown; *conidia* filiform, slightly curved to sickle-shaped, 12–23 × 1  $\mu$ m.

Chemistry. Thallus K-, C-, P+ yellow, UV- or  $\pm$  pale cream; TLC (solvents C and G): psoromic acid (specimens tested: holotype and *Ertz* 13021).

*Etymology. Isalonactis* refers to the remarkable Isalo Massif (type locality) and the close relationship to the genus *Lecanactis*.

Ecology and distribution. Isalonactis madagascariensis is known only from the type locality in Madagascar, situated 180 km from the nearest coast. It grows on sheltered siliceous rocks in an arid landscape, with a poorly-developed Roccella montagnei, a fruticose species widely distributed in the Palaeotropics and having a preference for coastal habitats (Tehler et al. 2010, including two specimens sequenced from the Isalo Massif). Other lichens collected from the same locality are Xanthoparmelia tananarivensis (Gyeln.) Hale, and members of the genera Buellia, Caloplaca, Pertusaria, Pyxine, Parmotrema, Toninia, Usnea and Xanthoparmelia. The type locality is situated just outside Isalo National Park which forms a Jurassic sandstone massif. The rocks have been subjected to erosion and form steep slopes and canyons. Isalo Massif is famous for its endemics. In addition to widespread Malagasy endemics such as Coleochloa setifera (Ridl.) Gilly (Cyperaceae) and Ischnolepis tuberosa Jum. & H. Perrier (Rubiaceae), numerous local endemic plant species are known from this area. Among palms (Dransfield & Beentje 1995), Ravenea rivularis Jum. & H. Perrier, R. glauca Jum. & H. Perrier and Dypsis onilahensis



FIG. 2. A–I, *Isalonactis madagascariensis* (A–C, E–I, holotype; D, *Ertz* 13021). A & B, thallus and apothecia; C, thallus bearing both soredia (white arrow) and apothecia (black arrow), and separated by a black, prothallus borderline from a sorediate thallus at the lower right corner of the photograph; D, thallus and soredia; E, section through an apothecium in water; F, conidia in water; G, ascus in KI; H & I, ascospores in water. Scales: A = 2 mm; B-D = 1 mm;  $E = 250 \text{ }\mu\text{m}$ ;  $F = 20 \text{ }\mu\text{m}$ ;  $G-I = 10 \text{ }\mu\text{m}$ . In colour online.

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(Jum. & H. Perrier) Beentje & J. Dransf. are almost restricted to Isalo. As members of the endemic families Asteropeiaceae and Sarcolaenaceae, the following shrubs are either endemic to Isalo or found in few other localities: Asteropeia labatii G. E. Schatz et al., Perrierodendron occidentale (Capuron) J. F. Leroy et al., Sarcolaena isaloensis Randrianasolo & J. S. Miller, S. oblongifolia F. Gérard, Schizolaena isaloensis Rabehevitra & Lowry, Xerochlamys undulata Hong-Wa and X. villosa F. Gérard (Ramananjanahary et al. 2010). Endemic or near endemic Xerophyta-species (Velloziaceae) are Xerophyta croatii Phillipson & Lowry, X. isaloensis Phillipson & Lowry, X. schatzii Phillipson & Lowry and X. setosa Phillipson & Lowry (Behnke et al. 2013). The sandstone rock outcrops are especially famous for numerous endemic succulents such as Pachypodium gracilius (H. Perrier) Rapan., Aloe isaloensis H. Perrier, Ceropegia dimorpha Humbert, C. pseudodimorpha Rauh, Cynanchum macrolobum Jum. & H. Perrier and C. rauhianum Descoings (Rauh 1995, 1998). The Isalo Massif also harbours a large number of endemic species of amphibians and reptiles (Crottini et al. 2008). It must be noted that the very peculiar Dermatiscum thunbergii (Ach.) Nyl. was found in a similar dry landscape, on a granitic inselberg opposite Anja Nature Reserve [12 km S of Ambalavao, 21°50′45·4″S, 46°50′21·8″E, 972 m, 5 October 2008, Ertz 12987 (BR), Sérusiaux s. n.(LG)]. This member of Physciaceae was only known from the southern part of continental Africa. It is newly recorded here from Madagascar.

Notes. As shown in our phylogenetic tree (Fig. 1), Isalonactis madagascariensis is most closely related to the genera Lecanactis and Chiodecton. It differs from Lecanactis by apothecia having a thalline margin with a pale brown hypothecium, whereas species of Lecanactis have a lecideine exciple with a usually dark brown to carbonized hypothecium. No species of Lecanactis are known to be sorediate. In the holotype specimen of Isalonactis madagascariensis, thalli might have either apothecia or soredia, but one thallus has both (Fig. 2C). In the specimen Ertz

13021, thalli are sorediate but one thallus has both soredia and apothecia, clearly indicating that sterile, sorediate morphs and fertile morphs are conspecific. Psoromic acid is rare in the genus Lecanactis, being known only in two species L. californica and L. dilleniana (Egea & Torrente 1994), but sequences obtained from the latter suggest that it belongs to another genus (D. Ertz, A. Tehler, M. Irestedt, A. Frisch, G. Thor & P. van den Boom, unpublished data). The ascomata of Isalonactis being sometimes undulated with a strongly folded margin might be reminiscent of the genera Chiodecton or Syncesia. However, Chiodecton species (represented in our phylogenetic tree by the only species for which sequences are currently available, i.e. C. natalense, and by a newly sequenced species, C. leptosporum) differ from our new genus by perithecioid to lirelliform ascomata aggregated into stroma-like structures, obovate or slightly biclavate ascospores and a different chemistry, roccellic acid (Thor 1990). The generic type, C. sphaerale Ach., still needs to be sequenced in order to confirm the phylogenetic position of the genus Chiodecton. However, that species has long, narrow  $(30-37 \times 2-3 \ \mu m)$  and obovate ascospores, and roccellic acid in the thallus (Thor 1990). Therefore it is most probably not congeneric with Isalonactis. The genus Syncesia forms a distinct, quite distantly related lineage to our new genus (Fig. 1; the generic type, S. myrticola, being included) and differs usually by curved, longer and slender ascospores in addition to a different chemistry (presence of protocetraric and roccellic acids in nearly all species, including the generic type) (Tehler 1997). The new genus and species might be reminiscent of the genus Sigridea due to the 3-septate ascospores lacking a gelatinous sheath, the thalline margin and the presence of psoromic acid. However, species of the latter genus differ from Isalonactis madagascariensis by a carbonized hypothecium and much shorter, up to 7 µm conidia (Tehler 1993). Moreover, the generic type of Sigridea (S. cali*fornica*) is phylogenetically not related to our new genus (Fig. 1). The sorediate thalli of our new taxon is similar to *Fulvophyton sorediata* (Sparrius *et al.*) van den Boom, but that species has immersed ascomata and very different ascospores, being (4-)6-8septate,  $20-35 \times 5-7 \mu m$  with a distinct gelatinous sheath *c.*  $3.5 \mu m$  wide (van den Boom & Giralt 2012). We also checked that no older generic names of *Arthoniales* were available to accommodate our new species.

Additional specimen examined. Madagascar: Isalo Massif near ANGAP house and National Park border, 851 m alt., 22°37'8·1"S, 45°21'42·6"E, Mesozoic sandstone cliffs with Coleochloa setifera, Ischnolepis tuberosa and Pachypodium gracilius, on sheltered rock, 7 October 2008, D. Ertz 13021, E. Fischer, D. Killmann, T. Razafindrahaja & E. Sérusiaux s. n. (BR, LG).

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