

## Standard Paper

# The strange case of *Ocellomma rediuntum* (Arthoniales: Roccellaceae) in Australia: a remarkably disjunct lichen

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### Abstract

The new combination *Ocellomma rediuntum* (Stizenb. ex Hasse) Kantvilas, Gueidan & Tehler is proposed, supported by morphological, anatomical and molecular data. Hitherto known only from the Californian coast, this species is here recorded for Kangaroo Island (South Australia), Victoria and Tasmania. It is described and illustrated from Australian collections. The ecology of the species and its remarkable distribution are discussed.

**Key words:** distribution, Kangaroo Island, lichens, *Schismatomma*, Tasmania, taxonomy, Victoria

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### Introduction

The order *Arthoniales* represents one of the largest groups of lichenized Ascomycetes. It comprises fruticose, foliose and crustose taxa and occurs in most ecosystems of the world, reaching its highest diversity in subtropical coastal habitats with a Mediterranean- or desert-type climate (Ertz & Tehler 2011). The group has had a chequered taxonomic history but the most recent classification (Ertz & Tehler 2011) recognized six families, including the *Roccellaceae*. This large family, estimated to comprise 28–42 genera and c. 300 species (Jaklitsch *et al.* 2016), includes taxa with (*inter alia*) a trentepohlioid photobiont, rounded ascomata with a thalline margin and reduced excipulum, cylindrical to clavate asci, and ascospores that lack a gelatinous sheath (Ertz *et al.* 2015). Features of the *Roccellaceae* as currently circumscribed are its high degree of species endemism and the relatively large number of small or monotypic genera, one of which is *Ocellomma* Ertz & Tehler, based on the Mediterranean taxon *O. picconianum* (Bagl.) Ertz & Tehler. Within the family, *Ocellomma* is characterized by a crustose, ecor-ticate thallus, erumpent, sessile, pruinose ascomata containing calcium oxalate, and hyaline, 3-septate ascospores, and was recognized as a distinct lineage on the basis of DNA sequence data (Ertz *et al.* 2015). In this paper, we record the North American species *Schismatomma rediuntum* ('*rediunta*') (Stizenb. ex Hasse) Tehler for southern Australia and Tasmania, and transfer it to the genus *Ocellomma* (*O. rediuntum* (Stizenb. ex Hasse) Kantvilas *et al.* comb. nov.) on the basis of morphological and anatomical data. Molecular data were also obtained and indicated that the widely separated Australian populations were conspecific.

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Whilst taxon sampling and support values were insufficient to categorically confirm the placement of this species within *Ocellomma*, they suggested a close affinity between it and *O. picconianum*. The remarkable disjunction between North American and Australian populations is discussed in the context of the ecology of the species.

### Materials and Methods

#### Anatomy, morphology and chemistry

The study is based chiefly on material collected by the first author in South Australia (Kangaroo Island) and Tasmania, and on herbarium material housed in AD, BM, FH, HO, MEL and S. Anatomical and morphological observations were undertaken using light microscopy, with thin hand-cut sections mounted in water, 10% KOH, lactophenol cotton blue, Lugol's iodine after pretreatment with dilute KOH, and ammoniacal erythrosin. Ascospore measurements are presented in the format: 5th percentile–average–95th percentile, with outlying values given in brackets and *n* being the number of measurements. Routine chemical analyses using thin-layer chromatography followed standard methods (Elix 2014). Calcium oxalate was observed by eluting thin sections in 20% sulphuric acid, which induces the precipitation of clusters of needle-like crystals. Terminology of asci follows Torrente & Egea (1989) as illustrated by Kantvilas (2004).

**Comparative specimen of *Ocellomma picconianum* examined.** Italy: Calabria, Crotona, near mouth of the River Neto, 39°13'N, 17°08'E, 5 m alt., on bark of *Eucalyptus*, 14 v 1989, D. Puntillo (*Lichenotheca Graecensis* 3, 57 (1996)) (BM).

#### DNA extraction, amplification and sequencing

Four Australian specimens of *Ocellomma rediuntum* (three from Tasmania and one from Victoria) were newly sequenced

(Table 1). Lichen material was detached from the substratum using clean tweezers and transferred to an Eppendorf tube. Genomic DNA was obtained using a phenol-chloroform-based protocol modified from Zolan & Pukkila (1986), as described in Gueidan *et al.* (2007). Three markers were amplified: the region including the 5.8S subunit of the nuclear ribosomal RNA gene and the internal transcribed spacers 1 and 2 (ITS), the large subunit of the nuclear ribosomal RNA gene (nrLSU), and the second largest subunit of the RNA polymerase II gene (*RPB2*).

The primers used for amplification were: ITS1F and ITS4 for the ITS region (White *et al.* 1990; Gardes & Bruns 1993), LR0R and LR5 for nrLSU (Vilgalys & Hester 1990) and *RPB2*-7cF and *RPB2*-11aR for *RPB2* (Liu *et al.* 1999). For the nuclear ribosomal regions, 1 µl of genomic DNA was added to a master mix comprising 5 µl of MyFi buffer (Bioline, London, UK), 1 µl of each primer, 1 µl of MyFi polymerase and 16 µl of water. For *RPB2*, the master mix was modified to include 2 µl of each primer. Amplifications were carried out on a Mastercycler Pro S thermocycler (Eppendorf, Hamburg, Germany) using standard PCR programs. PCR products were sent to Macrogen (Seoul, Korea) for purification and sequencing. Mixed and weak PCR products were cloned using a TOPO-TA cloning kit (Invitrogen, Thermo Fisher Scientific, Waltham, MA, USA) according to the manufacturer's instructions. Additional ITS, nrLSU and *RPB2* sequences were obtained for *Ocellomma picconianum* following previously described protocols (Tehler & Irestedt 2007; Tehler *et al.* 2009a, b, 2010).

### Phylogenetic analysis

Sequences were assembled using Sequencher v.5.4.6 (Gene Codes Corporation, Ann Arbor, MI, USA). *RPB2* and nrLSU sequences were aligned manually in Mesquite v.3.51 (Maddison & Maddison 2017), together with previously published sequences from various genera within *Roccellaceae* (mostly from Ertz *et al.* 2015) and some new sequences of *Ocellomma picconianum* (Table 1). For the combined nrLSU-*RPB2* analysis, two species of *Gyrographa* were used as an outgroup. The ingroup included our four Australian specimens of *O. rediuntum*, as well as 39 *Roccellaceae* taxa. To test for congruence, each locus (nrLSU and *RPB2*) was first subjected to a separate tree search and bootstrap analysis using maximum likelihood (ML) (RAxML VI-HPC v.8.2.9; Stamatakis *et al.* 2005, 2008), as implemented on the CIPRES Web Portal (<http://www.phylo.org>; Miller *et al.* 2010). A GTRCAT model was applied to the two markers. Support values were obtained using a fast bootstrap analysis of 1000 pseudoreplicates. Resulting topologies were compared for a potential conflict among loci using a 70% reciprocal bootstrap criterion (Mason-Gamer & Kellogg 1996). Because no conflict was detected, the two gene regions were concatenated, and the combined dataset analyzed using MrBayes v.3.2.6 (Ronquist *et al.* 2011).

The combined dataset had four partitions: *RPB2* first codon position, *RPB2* second codon position, *RPB2* third codon position and nrLSU. The models were estimated for each partition using MrModeltest v.2 (Nylander 2004). Two runs of four chains were carried out for 5 000 000 generations and trees were sampled every 500 generations. The convergence of parameters was checked with the program Tracer v.1.7.1 (Rambaut *et al.* 2014). The convergence of the average likelihood scores and topologies of all runs were also verified. A burn-in sample of 5000 trees was discarded for each run. The remaining 10 000 trees were used to estimate the posterior probabilities with the 'compute consensus' command

in PAUP\* v.4.0a (build 163) (Swofford 2002). The most likely tree was computed with the sumt command in MrBayes and visualized in PAUP\*. Additional support values were obtained using a fast bootstrap analysis of 1000 pseudoreplicates with RAxML, using the four previously described partitions.

Published and newly generated ITS sequences were also aligned using Mesquite but for a much smaller dataset due to the high variability of this locus across the *Roccellaceae*. This small dataset was combined with *RPB2* data with the aim of confirming the sister relationship between *O. rediuntum* and *O. picconianum*. For the ITS-*RPB2* dataset, two specimens of *Schismatomma pericleum* were used as an outgroup and the ingroup included *O. rediuntum* (3 specimens), *O. picconianum* (5 specimens), *Pseudoschismatomma rufescens* (2 specimens), two species of *Dirina*, and *Roccella allorgei*. A maximum likelihood tree search and bootstrap analysis were performed using RAxML as described above. Both LSU-*RPB2* and ITS-*RPB2* trees were visualized in PAUP\* and edited with Illustrator (Adobe Systems, San Jose, CA, USA). The datasets were deposited in TreeBASE (25482).

### Results

With the congruence test showing no conflict, the two markers nrLSU and *RPB2* were concatenated into a combined dataset. The resulting phylogeny is presented in Fig. 1, with posterior probabilities and bootstraps as support values. The recovered relationships were largely in agreement with the phylogeny of Ertz *et al.* (2015), with *Psoronactis*, *Lecanactis*, *Isalonactis* and *Chiodecton* forming early diverging groups. *Roccellina* clusters together with *Crocellina*, *Vigneronia*, *Dendrographa* and *Syncesia* (99% PP and ≤ 70% BS), and the lineage that includes *Diromma*, *Dirina* and *Roccella* is well supported (100% PP and BS). The four specimens of *Ocellomma rediuntum* form a monophyletic group (100% PP and BS). This species is resolved as sister to *O. picconianum* but the relationship is not supported (< 95% PP and ≤ 50% BS). Similarly, *Pseudoschismatomma* is resolved as sister to the lineage that includes *O. rediuntum* and *O. picconianum*, but this relationship is not supported (< 95% PP and ≤ 50% BS). The placement of the generic type of *Schismatomma* (*S. pericleum*) is neither resolved nor supported. The results of the combined ITS-*RPB2* analysis is shown in Fig. 2. This smaller dataset recovered full bootstrap support for the sister relationship between *O. rediuntum* and *O. picconianum* (100% BS), but insignificant support for *Pseudoschismatomma rufescens* as sister to these taxa (70% BS).

### Taxonomy

*Ocellomma rediuntum* (Stizenb. ex Hasse) Kantvilas, Gueidan & Tehler comb. nov.

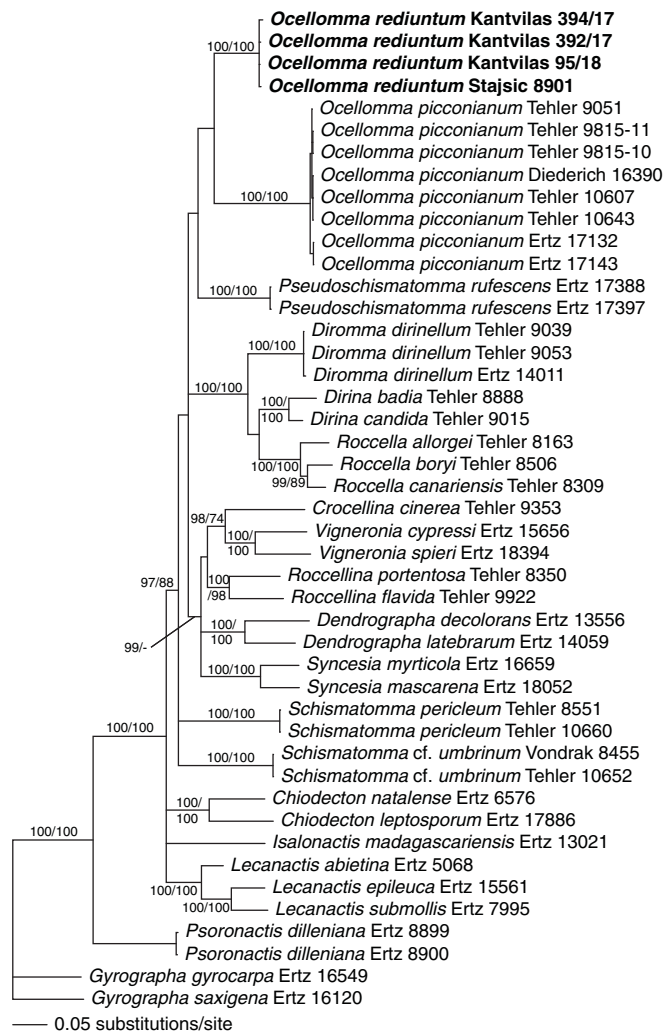
Mycobank No.: MB 833703

*Lecanora rediunta* Stizenb. ex Hasse, *Bull. Torrey Bot. Club* **24**, 446 (1897).—*Dirina rediunta* (Stizenb. ex Hasse) Zahlbr., *Ann. Naturhist. Mus. Wien* **16**, 82 (1901).—*Schismatomma rediuntum* ('rediunta') (Stizenb. ex Hasse) Tehler, *Lichenologist* **17**, 211 (1985); type: USA, California, Los Angeles Co., Santa Catalina Island, on *Heteromeles*, January 1895, Hasse (lecto, *vide* Tehler (1985))—UC; isolecto—UPS, US, W).

(Figs 3 & 4)

**Table 1.** Taxon sampling for the two phylogenetic analyses. The combined nrLSU and *RPB2* dataset included a total of 45 taxa and the combined ITS and *RPB2* dataset 15 taxa. Newly published sequences are indicated in bold. Dashes correspond to missing data and, for ITS, x indicates taxa not included in the dataset.

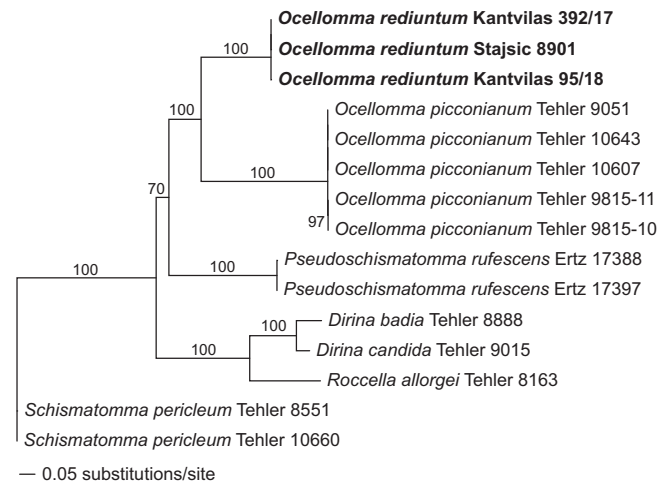
Taxon	Collection number (Herbarium)	nrLSU	<i>RPB2</i>	ITS
<i>Chiodecton leptospermum</i>	Ertz 17886 (BR)	KF831578	KF831579	x
<i>C. natalense</i>	Ertz 6576 (BR)	EU704085	EU704014	x
<i>Crocellina cinerea</i>	Tehler 9353 (S)	–	KJ524359	x
<i>Dendographa decolorans</i>	Ertz 13556 (BR)	HQ454607	HQ454747	x
<i>D. latebrarum</i>	Ertz 14059 (BR)	HQ454544	HQ454684	x
<i>Dirina badia</i>	Tehler 8888 (S)	KC108246	KC108050	KC107854
<i>D. candida</i>	Tehler 9015 (S)	KC108263	KC108067	–
<i>Diromma dirinellum</i>	Tehler 9039 (S)	KJ524287	KJ524366	x
<i>D. dirinellum</i>	Tehler 9053 (S)	KJ524288	KJ524367	x
<i>D. dirinellum</i>	Ertz 14011 (BR)	KJ524289	KJ524368	x
<i>Gyroglypha gyrocarpa</i> (outgroup)	Ertz 16549 (BR)	KJ524293	KJ524378	x
<i>G. saxigena</i> (outgroup)	Ertz 16120 (BR)	KJ524298	KJ524384	x
<i>Isalonnactis madagascariensis</i>	Ertz 13021 (BR)	KF831576	KF831580	x
<i>Lecanactis abietina</i>	Ertz 5068 (DUKE)	AY548812	AY552018	x
<i>L. epileuca</i>	Ertz 15561 (BR)	KJ524303	KJ524389	x
<i>L. submollis</i>	Ertz 7995 (BR)	EU704091	EU704023	x
<i>Ocellomma picconianum</i>	Tehler 9051 (S)	HQ454611	HQ454751	KF036024
<i>O. picconianum</i>	Tehler 9815-10 (S)	KF036039	KF036050	KF036025
<i>O. picconianum</i>	Tehler 9815-11 (S)	HQ454612	HQ454752	<b>MN811008</b>
<i>O. picconianum</i>	Tehler 10607 (S)	<b>MN811014</b>	<b>MN810322</b>	<b>MN811009</b>
<i>O. picconianum</i>	Tehler 10643 (S)	<b>MN811015</b>	<b>MN810323</b>	<b>MN811010</b>
<i>O. picconianum</i>	Diederich 16390 (BR)	HQ454613	HQ454753	x
<i>O. picconianum</i>	Ertz 17132 (BR)	KJ524312	KJ524399	x
<i>O. picconianum</i>	Ertz 17143 (BR)	KJ524313	KJ524400	x
<i>O. rediuntum</i>	Kantvilas 394/17 (HO)	<b>MN811011</b>	–	x
<i>O. rediuntum</i>	Kantvilas 392/17 (HO)	<b>MN811012</b>	–	<b>MN811005</b>
<i>O. rediuntum</i>	Kantvilas 95/18 (HO)	<b>MN811013</b>	<b>MN810320</b>	<b>MN811006</b>
<i>O. rediuntum</i>	Stajsic 8901 (MEL)	–	<b>MN810321</b>	<b>MN811007</b>
<i>Pseudoschismatomma rufescens</i>	Ertz 17388 (BR)	KJ524314	KJ524401	–
<i>P. rufescens</i>	Ertz 17397 (BR)	KJ524315	KJ524402	–
<i>Psoronactis dilleniana</i>	Ertz 8899 (BR)	KJ524316	KJ524403	x
<i>P. dilleniana</i>	Ertz 8900 (BR)	KJ524317	KJ524404	x
<i>Roccella allorgei</i>	Tehler 8163 (S)	EF081397	DQ987640	FJ639085
<i>R. boryi</i>	Tehler 8506 (S)	EF081398	DQ987641	x
<i>R. tinctoria</i>	Tehler 8309 (S)	EF081400	DQ987643	x
<i>Roccellina flavida</i>	Tehler 9922 (S)	HQ454592	HQ454732	x
<i>R. portentosa</i>	Tehler 8350 (S)	EF081446	DQ987689	x
<i>Schismatomma pericleum</i>	Tehler 8551 (S)	EF081451	DQ987694	KF036026
<i>S. pericleum</i>	Tehler 10660 (S)	KJ524323	KJ524410	–
<i>S. cf. umbrinum</i>	Vondrák 8455 (BR)	KJ524324	KJ524411	x
<i>S. cf. umbrinum</i>	Tehler 10652 (S)	–	KJ524412	x
<i>Syncesia myrticola</i>	Ertz 16659 (BR)	KJ524338	KJ524428	x
<i>S. mascarena</i>	Ertz 18052 (BR)	KJ524335	KJ524425	x
<i>Vigneronia cypressi</i>	Ertz 15656 (BR)	KJ524345	KJ524435	x
<i>V. spieri</i>	Ertz 18394 (BR)	KJ524348	KJ524440	x



**Fig. 1.** Phylogenetic placement of *Ocellomma rediuntum* within the *Roccellaceae*. Bayesian consensus tree of the combined nrLSU and *RPB2* dataset, with posterior probabilities and bootstrap values (PP/BS) above the branches. The outgroup consists of *Gyrographa* spp. and specimen information is presented in Table 1.

*Thallus* crustose, pale grey-white, scurfy, esorediate, ecorticate, rather patchy and uneven, at most to 80–100 µm thick, undelimited, containing calcium oxalate; medulla patchily KI+ pale violet; photobiont *Trentepohlia*, with cells coccoid, 10–20 µm diam.

*Apothecia* numerous, scattered, roundish, 0.2–0.5 mm wide, erumpent, broadly adnate, containing calcium oxalate; disc black, coarsely grey-pruinose, plane at first, later becoming convex; margin white, rather ragged and exfoliating in young apothecia, becoming somewhat excluded in the oldest, most convex apothecia, in section 10–15(–25) µm thick, lacking photobiont cells although sometimes with some thallus fragments adhering at the outer edge, dark brown, ±unchanged in K at the edge, somewhat paler within, KI–. *Hypothecium* 40–60(–90) µm thick, dark reddish brown, K+ olive, sometimes a little paler and patchily KI+ pale violet in the upper part. *Hymenium* hyaline, KI+ blue, 60–80 µm thick, overlain by a brownish epithecium to c. 20 µm thick, composed of minute granules that do not dissolve in K. *Asci* 50–65 × 13–20 µm, of the *myrtilcola*-type, typically 8-spored but sometimes with 2 spores aborted in mature asci. *Paraphyses* sparingly branched and anastomosed, 1–1.5 µm



**Fig. 2.** Phylogenetic relationships between *Ocellomma rediuntum* and *O. picconianum*. Most likely tree obtained with a combined ITS-*RPB2* dataset. RAXML bootstrap values are indicated above the branches. The outgroup consists of *Schimatomma pericleum* and specimen information is presented in Table 1.

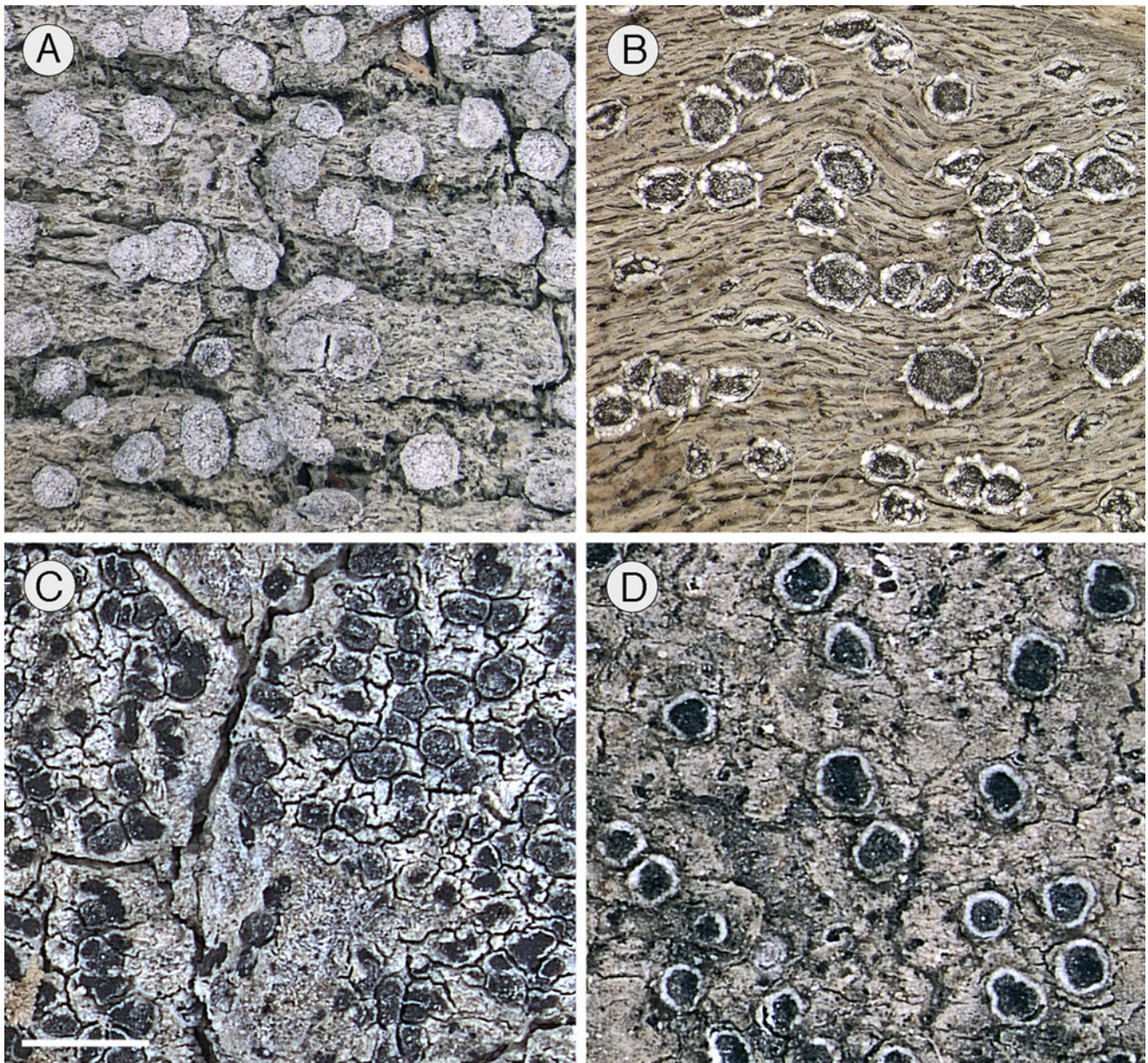
thick, with the apices minutely spinulose, barely expanded to c. 2–2.5 µm. *Ascospores* hyaline, non-halonate, 3-septate, fusiform, straight or curved, mostly a little attenuate at the distal end, (16–)17–20.9–25 × 4–4.6–5.5 µm ( $n = 60$ ).

*Pycnidia* usually numerous, visible as black, semi-immersed specks 0.05–0.1 mm wide; conidia bacilliform, straight or curved, 5–7 × 1–1.5 µm.

**Chemistry.** No substances detected by TLC.

**Remarks.** The above description is based exclusively on the Australian collections. It compares favourably with the description of Tehler (1993), based on North American collections, and our observations of a selection of these specimens. The morphology of the ascomata is variable. While the Tasmanian specimens have broadly adnate, superficial, discoid apothecia, specimens from the other provenances show apothecia ranging from neatly discoid to rather misshapen, and from semi-immersed to superficial (Fig. 3). However, no anatomical differences between these forms were observed. Ascospore size can vary from specimen to specimen and from section to section, but generally those spores retained in the ascus are smaller with thin walls and septa.

The affinities of the Australian collections to the genus *Ocellomma* were initially recognized on the basis of morphological and anatomical comparisons with herbarium material of *O. picconianum*. In his monograph of the genus *Schimatomma*, Tehler (1993) treated eight taxa, including those that were subsequently transferred to *Ocellomma* and other genera. Using this publication, the Australian specimens were identified to *Schimatomma rediuntum* on the basis of their esorediate thallus, erumpent, adnate, circular ascomata with a thin excipulum and pigmented hypothecium, 3-septate ascospores and bacilliform conidia. With respect to the general anatomy of the thallus, ascomata, asci and ascospores, these specimens also compared favourably with reference herbarium material of *O. picconianum*, a taxon which Tehler (1993) treated as a synonym of *Schimatomma dirinellum* but which Ertz et al. (2015) later placed in the separate genus *Diromma* Ertz & Tehler. *Schimatomma rediuntum* is a rare Californian species and no material could



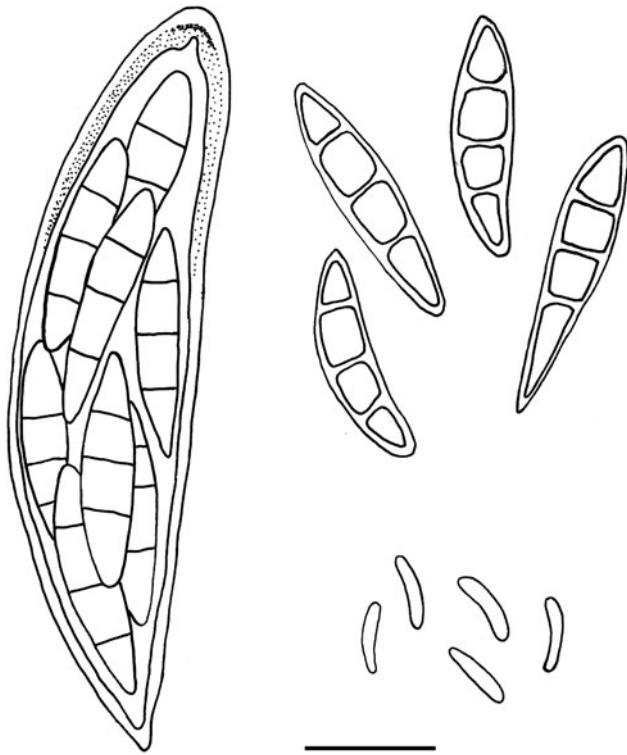
**Fig. 3.** Morphology of *Ocellomma rediuntum* showing regional variation. A, Tasmania; B, Kangaroo Island; C, Victoria; D, California. Scale = 1 mm. Photographs: Jean Jarman. In colour online.

be included in the phylogenetic study of Ertz *et al.* (2015). *Ocellomma picconianum* differs from that species chiefly by having a hyaline to pale hypothecium and by containing roccellic acid.

**Distribution and ecology.** *Ocellomma rediuntum* has been collected in Tasmania and Victoria, and on Kangaroo Island, South Australia, representing a remarkable range extension for a species hitherto known only from southern California (Tehler 1993).

In Tasmania, the species is known from three, widely separated localities. At one, on the island's east coast, it is locally very abundant on *Callitris rhomboidea* R. Br. ex Rich. in a narrow remnant stand along a seasonal creek (Fig. 5A). Although *C. rhomboidea* is a common and widespread tree in drier parts of Tasmania, small

'stands' where this species dominates are far less common. The stand where the *Ocellomma* was found is highly fragmented but is nevertheless of sufficient size to retain a rather unique complement of relatively unusual lichens on the oldest trunks and on some of the fallen logs (see also Baker *et al.* 2019). Indeed, several species previously unrecorded for Tasmania were found here, emphasizing the ecological significance of this vegetation type. These included *Hypocenomyce tinderryensis* Elix, *Lecanora casuarinophila* Lumbsch, *Ramboldia arandensis* (Elix) Kalb *et al.*, *Rinodina confusa* H. Mayrhofer & Kantvilas and *Usnea scabrida* Taylor subsp. *scabrida* (Baker *et al.* 2019; Elix *et al.* 2019). The *Ocellomma* thalli form extensive patches, tens of centimetres across, on the bark and wood of the oldest trunks as well as on smaller branches of old trees. It appears to favour somewhat drier microsites, where it is associated with *Schismatomma*



**Fig. 4.** *Ocellomma rediuntum*. Asci, ascospores and conidia, with amyloid tissues (after pretreatment with 10% KOH) stippled. Scale = 10  $\mu$ m.

*occultum* (C. Knight & Mitt.) Zahlbr., *Chrysothrix xanthina* (Vain.) Kalb, *Buellia reagenella* Elix, incipient thalli of *Austroparmelina conlabrosa* (Hale) A. Crespo et al. and *Usnea* species, and an unidentified species of *Opegrapha*.

The other Tasmanian localities are in *Melaleuca ericifolia*-dominated, swampy, coastal woodlands, a highly fragmented vegetation type of very significant conservation value for lichens (see Pérez-Ortega & Kantvilas 2018). Here, *Ocellomma rediuntum* grew on loose, papery *Melaleuca* bark; remarkably, at one site, it grew on the highly sheltered surface facing inwards towards the trunk (as distinct from outwards-facing). It was associated with *Bacidia septosior* (Nyl.) Zahlbr., *Cliostomum griffithii* (Sm.) Coppins and *Megalaria grossa* (Pers. ex Nyl.) Hafellner.

On Kangaroo Island, this lichen also displays a restricted and highly localized distribution. It was found in old stands of mallee and dry sclerophyll forest, where the abundance of large-stemmed dominant eucalypts and the diverse understorey of lesser trees and shrubs suggests that disturbance has been minimal and occurred a long time ago (Fig. 5B). *Ocellomma rediuntum* was found on the dead wood of old trunks, associated with *Cliostomum griffithii*, *Lecanora saligna* (Schrad.) Zahlbr., *Mycocalicium victoriae* (C. Knight ex F. Wilson) Tibell, *Opegrapha niveoatra* (Borrer) J. R. Laundon and an unidentified species of *Arthonia*. These collections were initially misidentified as *Schismatomma dirinellum* (Nyl.) Zahlbr. and reported under this name by Kantvilas (2018).

Naturally occurring, dry, sclerophyllous woodlands in temperate Australia are generally perceived to be a vegetation type where disturbance, especially in the form of frequent fires, is common. Often, they are also woodlands where clearing, grazing, firewood cutting and other human activities have occurred frequently. Thus

it is a rather poignant reminder that these woodlands can and do have old-growth characteristics, and that here the crustose *Roccellaceae* and their relatives can serve as indicators of ecological continuity, in much the same way as they do in forest types such as cool temperate rainforest, where other species of *Roccellaceae* (e.g. *Sagenidium molle* Stirt., *Lecanactis abietina* (Ach.) Körb., *L. latispora* Egea & Torrente, *Cresponea plurilocularis* (Nyl.) Egea & Torrente and *Lecanographa nothofagi* Kantvilas) tend to be closely associated with old trees and old forests (Kantvilas 2004).

The third Australian locality for *O. rediuntum* is also the most unusual in that here the lichen grew very abundantly on the bark of the exotic palm, *Washingtonia filifera* H. Wendl., in the National Botanic Gardens in urban Melbourne, Victoria (Fig. 6).

**Additional specimens examined.** **Australia:** South Australia, Kangaroo Island: the old cannery, American River, c. 1 km SW of Ballast Head, 35°46'S, 137°48'E, 3 m, 2013, G. Kantvilas 351/13 & B. de Villiers (HO); *ibid.*, 30 m, 2015, G. Kantvilas 487/15 (AD, HO); Grassdale Lagoon, 36°00'S, 136°53'E, 20 m, 2015, G. Kantvilas 346/15 & B. de Villiers (AD, HO, S). **Tasmania:** Stony Point, 40°45'S, 144°59'E, 2 m, 2016, G. Kantvilas 276/16 (HO); Wind Song Property, Callitris Gully, 42°21'S, 147°55'E, 40 m, 2017, G. Kantvilas 392/17 (BM, CANB, FH, HO, S); *ibid.*, G. Kantvilas 394/17 (HO, S); *ibid.*, 2018, G. Kantvilas 95/18 (CANB, HO); Cape Portland, Musselroe Wind Farm, northern end of Musselroe Bay, 40°48'36"S, 148°06'41"E, sea level, 2019, G. Kantvilas 243/19 (HO). **Victoria:** Royal Botanic Gardens, Melbourne, 37°49'52"S, 144°58'52"E, 2008, V. Stajsic 4862 (HO, MEL); *ibid.*, 2018, V. Stajsic 8901 (CANB, HO, MEL).—**USA:** **California:** Santa Monica Mountains, St Yuez Canyon, 1900, H. H. Hasse (FH); Santa Monica Mountains, Topanga Canyon, 1907, H. H. Hasse (FH); Catalina Island, 1906, H. H. Hasse (FH); *ibid.*, 1914, H. H. Hasse (FH); Santa Cruz Island, Prisoner's Harbor, 1994, A. Tehler 7411 (S); *ibid.*, along the track to Pelican Bay, 1994, A. Tehler 7376 (S).

## Discussion

Our study yielded morphological, anatomical and chemical data for discrete populations of *Ocellomma rediuntum* (from Kangaroo Island, Tasmania, Victoria and California) that supported the hypothesis that a single species is involved. Molecular data could be derived only from the Tasmanian and Victorian collections but supported their conspecificity. As noted by Tehler (1993), localities in the mainland Santa Monica Mountains in California have been impacted by urbanization and the species may well now be extinct in those areas; all other collections of *O. rediuntum* were made in the Channel Islands in the late 19th century and the beginning of the 20th century. Only two recent specimens from the Channel Islands are known, both collected by A. Tehler in 1994 from stands of *Quercus agrifolia* and *Q. dumosa* on Santa Cruz Island. Two other recent collections (San Clemente Island, 2014, K. Knudsen (UPS-L-691922); Monterey, 1998, S. Tucker 35997 (LSU-00149509)) were found to be misidentifications of *Lecanographa lyncea* (Sm.) Egea & Torrente s. lat. and *Dendrographa franciscana* (Zahlbr.) Ertz & Tehler, respectively.

Wide disjunctions and broad distribution patterns are not uncommon amongst lichens in general, although there are also examples where such apparent distributions have had to be reassessed as new data become available. Thus, Australasian



**Fig. 5.** Habitat of *Ocellomma rediuntum*. A, *Callitris rhomboidea*-dominated relict woodland, Tasmania; B, mature *Eucalyptus*-dominated mallee woodland, Kangaroo Island.

populations of the seemingly cosmopolitan, intertidal lichen, *Lichina confinis* (O. F. Müll.) C. Agardh, were found by Schultz (2017) to represent a different taxon, *L. intermedia* (C. Bab.) M. Schultz. At the same time, however, Muggia *et al.* (2013)

concluded that *Tephromela atra* (Huds.) Hafellner is indeed widespread, even though it displayed some infraspecific differentiation in various parts of the globe. Many widely distributed species are also rather weedy and opportunistic, for example *Amandinea*



**Fig. 6.** Habitat of *Ocellomma rediuntum*. Mature *Washingtonia* growing in the Royal Botanic Gardens, Melbourne. Photograph: Val Stajsic.

*punctata* (Hoffm.) Coppins & Scheid., *Gyalidea hyalinescens* (Nyl.) Vězda, *Lecanora dispersa* (Pers.) Sommerf., *Lecidella stigmataea* (Ach.) Hertel & Leuckert and *Peltigera didactyla* (With.) J. R. Laundon. Perhaps the best studied of these is *Xanthoria parietina* (L.) Beltr., and although Kondratyuk *et al.* (2007) described the Australian entity as *X. coomae* S. Y. Kondr. & Kärnefelt, Arup *et al.* (2013) remain equivocal as to whether this taxon is truly distinct. There are also well-known examples of bipolar species (e.g. *Alectoria nigricans* (Ach.) Nyl. and *Cetraria aculeata* (Schreb.) Fr.) and pan-temperate species (e.g. *Cliostomum griffithii* (Sm.) Coppins and *Thelotrema lepadinum* (Ach.) Ach.). The distribution of these is interpreted as being linked to a discrete climatic zone

(e.g. boreal versus austral), or habitat (e.g. old-growth forests). It remains to be seen whether these distributions and taxonomic interpretations stand up to detailed molecular investigation but, for the present, there is no suggestion that the separate geographical populations should be recognized as different taxa. Other widely distributed species, especially those with asexual propagules, are often seen as examples of long-distance dispersal by wind, birds and other vectors. Numerous austral lichen distributions have been interpreted in this way by Jørgensen (1983) and Galloway (1979).

Perhaps of greatest interest are disjunct or widely distributed species that are also very rare and/or have narrow ecological niches. A good example is *Culbersonia nubila* (Moberg) Essl., which was first described from East Africa and Saudi Arabia (Moberg 1980), then found in Tasmania (Kantvilas 1991), and is now recorded more widely, chiefly in the dry subtropics (Obermayer *et al.* 2009). Although widely distributed, this species cannot be considered common and is linked to a very discrete microhabitat.

In the light of this discussion, the distribution of *O. rediuntum* is highly curious. Disjunctions of the magnitude proposed here for this species have not been described previously for any species in the *Roccellaceae*. Perhaps one of the more remarkable examples from this family is that of *Lecanographa uniseptata* Ertz *et al.*, which is known to occur only in Gabon, Central Africa, and Guatemala, Central America (Ertz *et al.* 2010). Another interesting case is the genus *Angiactis*, known only from southern Australia, Bermuda and the Galapagos, but in this case, the three widely separate populations are accorded species rank, albeit on the basis of rather subtle differences (Aptroot *et al.* 2008). A disjunct occurrence between Kangaroo Island, Tasmania and California could be interpreted as a relict pattern of an old-growth dependent species in a Mediterranean, perhaps circum-Pacific setting. Several species of the saxicolous foliose genus *Xanthoparmelia* Hale exhibit American-Australian disjunctions (Nash & Elix 2004). The occurrence of *Ocellomma rediuntum* on Kangaroo Island and Tasmania is certainly suggestive of an old-growth species surviving in a relict vegetation type. Whilst it is not possible to reconstruct its Californian ecology, the habitat as described by Tehler (1993) could also be a relict dry forest. However, the Victorian locality in the Royal Botanic Gardens in urban Melbourne poses the most interesting question. The provenance and history of the individual host plant is unknown but, coincidentally, *Washingtonia* is native to California. Perhaps the epiphytic *Ocellomma* is an accidental introduction that arrived with its host? However, if this were the case, it is impossible to imagine that the Kangaroo Island and Tasmanian populations could be derived from this 'pioneer' source. Introductions are neither infrequent nor impossible in plants but the organism involved usually remains either limited to its locus of arrival or becomes adventive and spreads widely. The fact that *O. rediuntum* is not known from anywhere else in Australia (yet it is relatively conspicuous) does not suggest a weedy or adventive species. In the same way, it seems inconceivable that *Ocellomma* spread from natural woodland to a planted, urban *Washingtonia* without also establishing somewhere else. Thus, the distribution of this enigmatic species remains a mystery and awaits the discovery and analysis of further populations. Of particular interest would be North American collections that might yield molecular data.

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