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A new eight-spored species of *Menegazzia* from Australia

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Abstract: The new species, *Menegazzia jamesii* Louwhoff & Kantvilas from Victoria and Tasmania, closely related to *M. pertransita* (Stirt.) R. Sant., is described. Chemical and nomenclatural notes on *M. caliginosa* P. James & D. J. Galloway and *M. pertransita* are provided, and the new combination, *M. stirtonii* (Zahlbr.) Kantvilas & Louwhoff, is proposed. The name *M. weindorferi* (Zahlbr.) R. Sant., widely applied in Australian literature, is considered synonymous with *M. pertransita*, whereas *M. bullata* (Stirt.) Bitter is considered a synonym of *M. stirtonii*.

Key words: Australia, *Menegazzia*, pigments

Introduction

The lichen genus *Menegazzia* was introduced by Massalongo (1854) for the widespread, Northern Hemisphere species *M. terebrata* (Hoffm.) A. Massal. However, by far the greatest speciation in the genus occurs in the Southern Hemisphere, and centres of diversity for *Menegazzia* are found in southern South America (Santesson 1942; Adler & Calvello 1996; Bjerke 2001; Bjerke & Elvebakk 2001), New Zealand (Galloway 1983; James 1985), southern Australia and Tasmania (Kantvilas & James 1987; James & Galloway 1992) and Papua New Guinea (James *et al.* 2001). The genus thus displays a typical austral cool temperate world distribution (Galloway 1979), occurring on land masses derived from the ancient supercontinent of Gondwana. It tends to favour moist, cool habitats, especially at higher elevations, occurring commonly in cool temperate rainforest vegetation where the genus *Nothofagus* predominates, or in associated woodlands and heathlands. With an estimated 60 species (James & Galloway 1992), very few of which occur north of the equator, for example in Taiwan (Aptroot *et al.* 2003) and the Neotropics (Bjerke 2002), *Menegazzia* is in some respects the biogeographical antithesis of the genus *Cetraria* Ach. s. lat., which is very species rich in the Northern Hemisphere but with very few species in the Southern Hemisphere.

Characteristic features of *Menegazzia* are a foliose thallus, typically perforated with prominent holes in the upper surface (although a few species are eperforate), a hollow medullary cavity, a glossy, black, erhizinate lower surface with the thallus attached to the substratum by knob-like bulges of the lower cortex, typically prominently cupulate, lecanorine apothecia, thick-walled ascospores and netted paraphyses. Species tend to be characterized by general morphology, the number of spores per ascus, the absence or presence and morphology of soralia, and by chemical composition.

The history of the genus *Menegazzia* was reviewed briefly by Santesson (1942). Poelt (1974) was the first to propose that *Hypogymnia* and a number of other

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genera, including *Menegazzia*, should be accommodated in a separate family, the *Hypogymniaceae*, a name validated by Elix (1979) but then only containing *Hypogymnia*. Park (1990) also placed it in the *Hypogymniaceae* alongside *Hypogymnia*, apparently based on a superficial resemblance to this genus, which also has a naked, black under surface and often hollow lobes. However, Kärnefelt & Thell (1992) and Thell *et al.* (1995) showed that asci and hamathecial structures differ appreciably between the two genera, and that *Menegazzia* diplays some similarities to the fruticose genus *Alectoria*: thick-walled, sometimes pigmented and rather large ascospores, densely branched and anastomosing paraphyses and very prominently apically thickened asci, features unusual for the *Parmeliaceae*. More recently, *Menegazzia*, *Hypogymnia* and the *Alectoriaceae* have been re-incorporated into the *Parmeliaceae* (Eriksson *et al.* 2003; Mattsson & Wedin 1999; Wedin *et al.* 1999). Although it is not within the scope of the current paper to comment on the taxonomic position of *Menegazzia*, it would be of interest for this genus to be included in future molecular studies into the phylogenetic relationships of the *Parmeliaceae*. Such studies support the inclusion of *Hypogymnia* within the *Parmeliaceae* (Crespo & Cubero 1998; Crespo *et al.* 1999), but have not been carried out for *Menegazzia*.

Vainio (1890) recognized that species of *Menegazzia* possess either two-spored or eight-spored asci, and this infra-generic division was formalized by Santesson (1942) who described the subgenera *Octospora* and *Dispora*. The eight-spored species are known only from the southernmost parts of the world and are the focus of the present study. New Zealand in particular appears to have a high diversity of eight-spored, primary species (that is, species lacking asexual propagules): *M. dielsii* (Hillman) R. Sant., *M. foraminulosa* (Kremp.) Bitter, *M. pertransita* (Stirt.) R. Sant. and *M. pulchra* P. James & D. J. Galloway. Here we describe a new species from southern Australia and Tasmania. We also provide notes on several other species, and clarify the nature of some of the yellow medullary pigments that they contain.

Methods

The study is based on the personal collections and field observations of the authors and on material held in BM, HO and MEL. Observations of thallus and apothecial anatomy were undertaken using low-power and high-power microscopy. Chemical analyses were undertaken by thin-layer chromatography using standard methods (Orange *et al.* 2001) and by spot tests with 15% KOH. Selected specimens were analysed chemically by Prof. J. A. Elix, Canberra, using high-performance liquid chromatography (Feige *et al.* 1993).

The New Species

Menegazzia jamesii Louwhoff & Kantvilas sp. nov.

Menegazziae pertransitae valde similis et item acidum lichesterinicum continens et ascos octosporos habens, sed lobis dense imbricatis contortisque, interdum longitudinaliter porcatis, et praecipue pigmentum aureum 'pigmentosinum' ad apices loborum continentibus differens.

Typus: Australia, Victoria, Mt Donna Buang, *c.* 20 km N of Warburton, near summit carpark, 37°42′S 145°41′E, *c.* 1200 m altitude, May 1993, *S. Louwhoff* 44 (BM—holotypus; HO, MEL—isotypi).

(Fig. 1)

Thallus tightly adnate, forming irregular rosettes to 10–20(–30) mm wide, lacking soredia or isidia. *Lobes* hollow, inflated, 1–4 mm wide; central lobes very densely imbricate, contorted and rather twisted, sometimes ± ridged, with numerous, interwoven secondary lobes and lobules; marginal lobes radiating, contiguous or discrete, irregularly dichotomous or ± palmate. *Upper surface* perforate, dull pale greenish grey with a bluish hue when fresh and moist, greyish white to cream when dry, smooth to weakly rugulose. *Perforations* abundant, round or irregularly oval-shaped, 0·5–1·5 (–3) mm wide, with margins flush with the surface or inrolled, sometimes markedly so. *Medullary cavity* on the upper side white to cream, usually sparsely and irregularly streaked or speckled with patches of a coarse, bright yellow to yellow-orange,

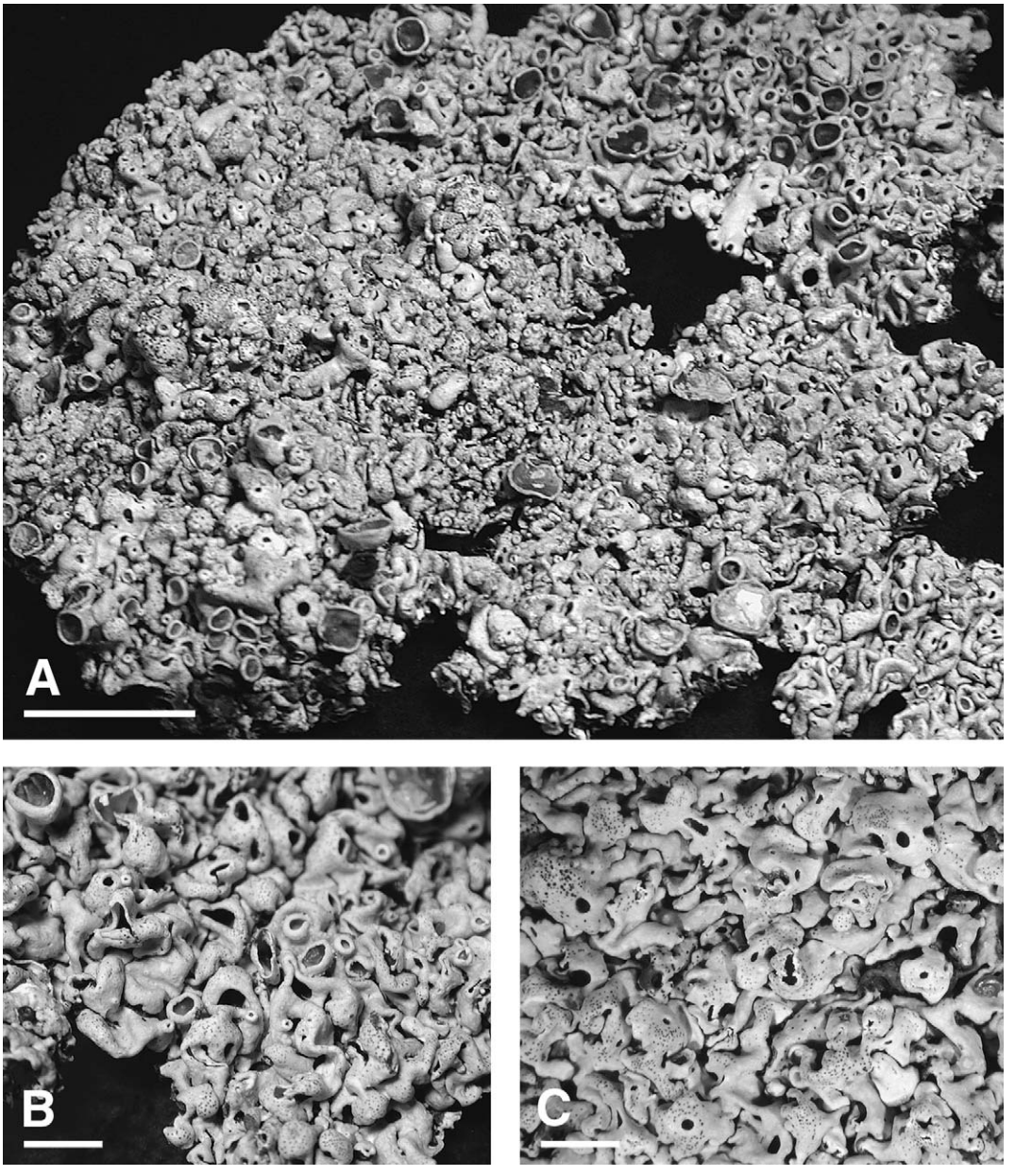

FIG. 1. *Mengazzia jamesii* (isotype in HO). A, habit; B, detail, showing contorted, crowded lobes with ridges; C, detail, showing tightly overlapping lobes. Scales: A=20 mm; B & C=5 mm.

K+purple pigment, especially at the tips of the lobes or sometimes beneath the apothecia; lower side of medullary cavity purplish grey. *Lower surface* wrinkled, membranaceous, glossy, black, becoming paler brown towards the lobe tips.

Apothecia typically abundant, scattered or clustered, (1·5–)2–7(–9) mm wide,

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irregularly roundish, sessile to subpedicellate; thalline margin thick (up to 1 mm) and inrolled when young, becoming thinner with age (*c.* 0·1–0·2 mm), mostly smooth and entire with occasional, rather faint, radial fissures, becoming scabrous when old; disc orange-brown to pale brown, convex at first, becoming plane to undulate, frequently markedly eroded in older apothecia. *Hymenium* (80–)110–140 µm thick, colourless in the lower part, pale reddish brown, non-granular above, ± pale yellowish brown to colourless in KOH. *Asci* ellipsoid to broadly obclavate, (60–)70–90 × 40–50 µm, sometimes protruding through the upper surface of the disc but more commonly nestled deeply within the hymenium and surrounded by a web of intricately branched and anastomosing paraphyses, eight-spored when young, but usually with 2 or more ascospores aborting during development. *Ascospores* simple, hyaline, ellipsoid (often irregularly squashed when in the ascus), 26–38(–42) × 17·5–25(–28) µm; walls 3–6 µm thick.

Pycnidia numerous, visible as dark brown or black specks *c.* 0·1 mm wide, scattered mainly on the central lobes. *Conidia* filiform, 6–8 × 1·8 µm.

Chemistry. Cortex K+ yellowish, KC −, C −, P −, UV −; white parts of medulla K −, KC −, C −, P −, UV −; yellow-pigmented parts of medulla K+ deep purple, KC −, C −, P −, UV+ orange. Containing atranorin and chloroatranorin (usually trace only), lichesterinic acid, protolichesterinic acid, strepsilin (±), pigmentosin A (irregularly distributed in the thallus). Other fatty acids such as isonephrosterinic, nephrosterinic and homolichesterinic acids are also sometimes present but are part of the same lichesterinic acid chemosyndrome (J.A. Elix pers. comm.).

Etymology. It is a pleasure to name this species in honour of Peter Wilfred James, a friend and mentor to us both. The name of Peter James has long been associated with the genus *Menegazzia*, and he has undertaken pioneering work on the taxonomy of the genus in many parts of the world, collecting and naming many species for the first time.

Remarks. Menegazzia jamesii is a very enigmatic species and although relatively frequently collected (especially from Mt Donna Buang, Victoria), it has been confused in the past with the related taxon, *M. weindorferi* (now referred to *M. pertransita*, see below). Indeed, recognition of its distinct status has required considerable study of a wide range of specimens, both in the field and in herbaria. The critical, unequivocal character that defines this species is the presence of the bright orange-yellow, K+ purple pigment, pigmentosin A. However, the occurrence of this substance, in entire local populations of *M. jamesii* (such as might occur on a single tree trunk) or even in a single thallus, is very patchy. It is typically found on the upper surface of the medullary cavity at the tips of marginal lobes, forming irregular streaks, patches or specks, but individual lobes or thalli may be entirely unpigmented. The pigment is not easily detected by chromatographic techniques but can be readily seen with the naked eye or under low-power magnification by slicing away the black lower cortex of young lobes to expose the white medullary cavity. The pigment is not to be confused with the distinctly paler, suffused yellowish secalonic acid or eumitrin pigments that occur in *M. pertransita*; these are K − or K+ weakly reddish. Nor is it to be confused with emodin type pigments that are also K+ purple, UV+ orange and are found together with stictic and echinocarpic acids in *M. caliginosa* and *M. foraminulosa*.

There are also subtle but consistent morphological differences that separate *M. jamesii* from *M. pertransita*. The entire thallus of the former tends to be coarser and larger with a bulkier, more inflated appearance, and the lobes are very densely imbricate, entwined and contorted (Fig. 1A & C). The lobes of *M. pertransita* are less intertwined and it is usually not difficult to discern individual lobes extending across a

thallus (Fig. 2). Furthermore, in *M. jamesii*, the lobes tend to be twisted and often have a longitudinal ridge (Fig. 1B), whereas in *M. pertransita*, ridges are rather infrequent and the lobes tend to remain ± tubular in cross-section. Secondary lobes occur in both species but in *M. jamesii* these are very tightly intertwined, further contributing to the impression that the thallus is very tightly contorted. Nevertheless, these two species are easily confused and mixed collections may be encountered; for example the specimen in MEL of *Lichenes Australasici Exsiccati* 162 contains fragments of both. However, given some experience, when confronted with both taxa growing in close proximity in the field, their separation is not difficult.

A minor chemical difference between the two taxa that requires further exploration is the occasional presence of strepsilin in *M. jamesii*. This compound does not seem to occur in *M. pertransita*. Furthermore, in the single Tasmanian specimen of *M. jamesii*, minute traces of stictic and constictic acids were detected by HPLC (J. A. Elix, pers comm.); an anomaly as yet unexplained.

Distribution and ecology. *Menegazzia jamesii* is known from moist, highland, wet sclerophyll forest and cool temperate rainforests in southern Victoria where it may be locally common. Here it grows on the trunks of *Acacia obliquinervia* Tindale and *Nothofagus cunninghamii* (Hook.) Oerst. in open sunny habitats, such as at the forest edge, along roadsides and in forest gaps. Associated lichens include the morphologically similar and closely related *Menegazzia pertransita*, *Parmelia tenuirima* Hook.f. & Taylor, *Hypogymnia enteromorphoides* Elix and species of *Usnea*. The new species is rare in Tasmania and known from a single collection from Mt Scott in the north-eastern highlands. Here it grew in a rather unusual habitat, on the trunk of a very old, solitary *Nothofagus cunninghamii* tree in a highland grassland that is being re-invaded by *Leptospermum* following the cessation of burning by Tasmania's indigenous inhabitants almost two centuries ago. As such it may well represent a relict of a past ecological regime where *Nothofagus* occurred as scattered trees in a very open environment; today this tree tends to occur only in closed rainforest.

Additional specimens examined. **Australia:** *Victoria*: Cement Creek, Mt Donna Buang, 5 v 1976, *D. G. Reid* (BM); Mt Donna Buang, 1993, *G. Kantvilas* 118/93, *P. McCarthy & S. Louwhoff* (HO); Otways Region, Aire Valley Track, 2 xi 1997, *S. Ford* (HO); Turtons Way near Beech Forest, 1969, *G. C. Bratt & R. C. Weeks* 69/789 (HO); near Healesville, Cumberland Falls, 5 iv 1976, *D. G. Reid* (BM); same locality, 1981, *R. B. Filson* 17249 (MEL); Goonmirk Rocks, Errinundra Flora Reserve, 1986, *J. A. Elix* 19948 & *H. Streimann* p.p. (*J. A. Elix: Lichenes Australasicia Exsiccati* 162) (MEL); Mt Ellery, xi 1960 (collector unknown) (MEL). *Tasmania*: summit ridge of Mt Scott, 2002, *G. Kantvilas* 229/02 (HO).

Notes on related taxa

Menegazzia caliginosa P. James & D. J. Galloway

New Zealand J. Bot. **21:** 194 (1983); type: New Zealand, Canterbury, Craigieburn Forest Park, track from Information Centre to Lyndon Saddle, 1000–1100 m, on bark of *Nothofagus solandri* var. *cliffortioides*, ix 1981, *P.W. James* (holotype—BM!).

For a complete description of this eight-spored sorediate species, see James (1985) and James & Galloway (1992). *Menegazzia caliginosa* has a very characteristic chemistry that comprises atranorin, chloroatranorin, stictic acid (major), constictic acid (minor), echinocarpic acid (major), cryptostictic acid (minor), peristictic acid (trace), menegazziaic acid (minor), conechinocarpic acid (minor), subechinocarpic acid (minor) and the orange-yellow pigments, 7-chloroemodin and flavo-obscurin B1 (K+ purple, UV+ orange) (J.A. Elix, *in litt*.). Essentially the same chemistry is found in *M. foraminulosa* (Kremp.) Bitter, its fertile, non-sorediate counterpart. *Menegazzia caliginosa* is very distinctive, even apart from its unusual chemistry. The thallus often has a greenish tinge (*M. pertransita* and its relatives are more often bluish) and the lobes are frequently white maculate at the tips and also rather flattened, giving the appearance of having a discontinuous, black margin when viewed from above. The emodin

pigment occurs in a thin, continuous layer on both the upper and lower sides of the medullary cavity, whereas in *M. jamesii*, the pigment (in this case pigmentosin) is very patchy and found only on the upper surface. *Menegazzia caliginosa* is known from Tasmania, where it is very rare and confined to cool temperate rainforest, from Victoria where it was first recorded by Ford (2001) and from New Zealand. Fertile specimens have been encountered only in New Zealand.

Selected specimens examined. **Australia:** *Victoria*: Errinundra National Park, Coast Range Road, 4 iv 1999, *S. Ford* (MEL). *Tasmania*: Little Fisher River, 20 x 1984, *G. Kantvilas* 702/84 (BM, HO); Sumac Spur 2, south of Arthur River,1981, *G. Kantvilas* 293/81 (BM, HO); Green Head, SSE of Greystone Bluff, 1991, *G. Kantvilas* 76/91 (HO).—**New Zealand:** *South Island*: Cass Hill, 7 ix 1981, *F. J. Walker* (BM); Mt Cook National Park, Governors Bush, 26 xi 1983, *F. J. Walker* (BM).

Menegazzia pertransita (Stirt.) R. Sant.

Ark. Bot. **30A** (11)**:** 12 (1942).—*Parmelia pertransita* Stirt., *Proc. Phil. Soc. Glasg.* **10:** 294 (1877); type: New Zealand, near Wellington, *J. Buchanan* (holotype—BM!).

Menegazzia weindorferi (Zahlbr.) R. Sant., *Ark. Bot.* **30A** (11)**:** 12 (1942).—*Parmelia weindoferi* Zahlbr., *Ann. Mycol.* **4**: 489 (1907); type: Tasmania, ad corticem arborum frondosarum in monte Roland, *G. Weindorfer* (*A. Zahlbruckner: Lichenes Rariores Exsiccati* n. 95) (syntype—BM!).

Parmelia weindorferi f. *endocitrina* Hillm., *Feddes Repert.* **45**: 172 (1938); type (*n.v.*).

Parmelia amabilis Zahlbr., *Denkschr. Akad. Wiss, Wien math.-naturwiss. Kl.* **104**: 359 (1941); type: New Zealand, Otago, Silver Peaks near Dunedin, on *Nothofagus solandri* var. *cliffortioides*, January 1934, *J. S. Thomson* ZA 206 (holotype—W).

(Fig. 2)

This species is characterized by ± swollen, loosely to intricately interwoven, abundantly perforate lobes, subpedicellate to sessile apothecia with a smooth or frequently radially cracked and scabrid thalline margin, eight-spored asci and a chemical composition comprising atranorin, chloroatranorin, lichesterinic and protolichesterinic acids as the major lichen substances. The

FIG. 2. *Menegazzia pertransita*, habit (*Kantvilas* 373/03). Scale = 10 mm.

upper surface of the medullary cavity, especially at the lobe tips, is either white or with a patchy, diffuse yellowish, K − or K+ reddish pigment. The composition of the pigment is variable, but those specimens analysed (by Prof. J.A. Elix) contain either eumitrins or secalonic acid derivatives (or both) in varying combinations. A comprehensive description of this species is provided by James (1985).

There has long been some conjecture regarding the putative differences between *M. pertransita*, based on a type from New Zealand, and *M. weindorferi,* based on a Tasmanian type specimen (for example, see James 1985, James & Galloway 1992). Our investigations, involving chemical analyses and morphological and anatomical examination of a wide range of specimens from New Zealand, Tasmania and southern mainland Australia have convinced us that the two taxa are conspecific. Morphological characters, such as the nature of the thalline exciple and degree of interweaving of the lobes, vary greatly in this species. The degree of pigmentation is also very variable. In general, most New Zealand material studied is pigmented to a greater or lesser extent, whereas in Tasmania and Australia, the occurrence of the pigment is variable and numerous collections are unpigmented or almost so. Clearly the presence of pigment has caused problems to taxonomists in the past; hence, for example, the description of the

pigmented form *M. weindorferi* f. *endocitrina* by Hillman (1938), based on a New Zealand type. Chemical analyses have proved very tricky in this species, not least because of the low concentration of many of the compounds and their variable occurrence in different portions of a single thallus. Thus we have found all the key compounds, that is, atranorin, chloroatranorin, lichesterinic acid and protolichesterinic acid, to be sometimes absent or present in only trace concentrations. The pigments are also very weak and typically streak in thin-layer chromatography so that, as in *M. jamesii*, their detection is probably best undertaken using low-power magnification.

Menegazzia pertransita is widespread and common in the region, especially Tasmania where it is often one of the dominant epiphytes on the young branches and trunks of trees in cool temperate rainforest, associated with species of *Parmelia, Pertusaria, Hypogymnia, Usnea* and other pale grey or brightly coloured lichens.

On the basis of herbarium material only (and not a study of type specimens) the southern South American species, *M. albida* (Zahlbr.) R. Sant. (=*M. wilsonii* Räs.) appears to be very closely related to *M. pertransita* and contains the same suite of fatty acids. However, we have found no pigments whatsover in any specimens seen. Further study of this taxon may find that it too is conspecific with *M. pertransita* but, in any event, the Australasian name has priority and such an outcome would have no nomenclatural implications for Australasian lichenologists.

Selected specimens examined. **New Zealand:** *South Island*: Lewis Pass, 29 iv 1997, *W. Malcolm & A. Vězda* (*A. Vězda: Lichenes Rariores Exsiccati* 283) (BM, HO); Cass, *G. E. & G. Du Rietz* 1462:4a (HO); Greyneyes Flat, 1985, *J. A. Elix* 19007 *& J. Johnston* (*Lichenes Australasici Exsiccati* 109) (BM); Haast Pass, Mt Brewster, 1962, *P. W. James* s.n. (BM).—**Australia:** *Victoria:* along road to Lake Mountain, 5 x 1983, *G. Kantvilas* s.n. (HO); near Marysville, Cumberland Falls, 15 xii 1960, *S. Thrower* (BM). *Tasmania*: Savage River Pipeline Road, 1980, *G. Kantvilas* 724/80 (BM, HO); Lake Hwy near Projection Bluff, 1980, *G. Kantvilas* 165/80 (BM, HO); Dohertys Cradle Mountain Hotel grounds, 2003, *G. Kantvilas* 373/03 (HO).

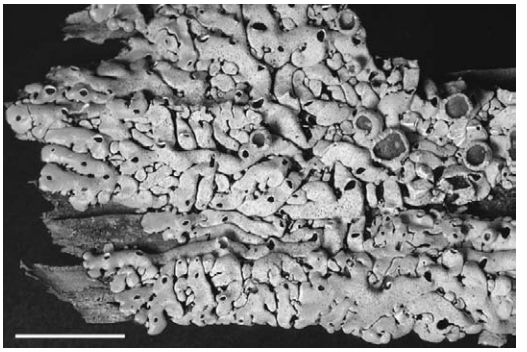

FIG. 3. *Menegazzia stirtonii*, habit (*J. Rowlands* s.n.). Scale=10 mm.

Menegazzia stirtonii (Zahlbr.) Kantvilas & Louwhoff comb. nov.

Basionym: *Parmelia stirtonii* Zahlbr., *Cat. lich. univ.* **6** (1)**:** 57 (1929); type: New Zealand, 'ad ramos prope Wellington', *J. Buchanan*, rec'd March 1882 (holotype—BM!).

Parmelia bullata Stirt., nom. illeg., *Trans. N.Z. Inst.* **32:** 79 (1900).—*Menegazzia bullata* (Stirt.) Bitter, *Hedwigia* **40:** 267 (1901); type as for *P. stirtonii* Zahlbr. (above).

(Fig. 3)

This species was not included by Galloway (1985) and Malcolm & Galloway (1997) in their accounts of the New Zealand lichen flora, but is a well-defined taxon, albeit with a confused taxonomy. *Parmelia bullata* Stirt. (Stirton 1900) is a later homonym of *Parmelia bullata* (Sw.) Ach. (Acharius 1803: 224), a species of *Leptogium;* hence this name is illegitimate and must be rejected. Zahlbruckner (1929) recognized this and introduced the new name, *P. stirtonii* Zahlbr, based on the same type. Whereas under Article 7.3 and Article 58 of the *Saint Louis Code*, there could be a possibility of retaining the name '*Menegazzia bullata* Bitter', it would seem more appropriate to introduce a new combination based on *P. stirtonii* Zahlbr. This is especially so because the use of '*M. bullata*' by Bitter (1901) was provisional (see Article 34.1) and not based on an examination of any original material.

Based on a single relatively recent collection of this species (housed in MEL) and the small, fragmented type specimen in poor condition, the following diagnostic characters can be discerned: thallus upper surface slightly wrinkled; apothecia 3–5 mm wide, with prominent, rather swollen, inrolled thalline margin; epithecium dark red-brown, *c.* 10 µm thick, becoming fuscous brown in KOH, with the apices of the paraphyses remaining persistently pigmented; hymenium *c.* 130 µm thick; asci eight-spored; ascospores 28–44 × 16–25 µm; chemical composition comprising atranorin, norstictic acid (major), echinocarpic acid (major) and connorstictic acid. The presence of norstictic acid is evident in squash preparations where red, needle-like crystals appear in the subhypothecial and excipular medulla with the addition of KOH. This character and the fuscous epithecium were also noted by Stirton (1900) in his original description. The rather thick apothecial margin is similar to that found in the Tasmanian endemic *M. corrugata* P. James, but that species has two-spored asci and contains stictic acid. Norstictic acid is relatively uncommon in *Menegazzia* in Australasia (most contain stictic acid) but is found also in *M. norstictica* P. James. This species differs from *M. stirtonii* by its two-spored asci and thinner apothecial margin. Echinocarpic acid is also relatively uncommon, but occurs in *M. caliginosa* and *M. foraminulosa*. These species also have paraphyses with pigmented apices but differ in having stictic acid as the major medullary compound and also contain emodin type medullary pigments.

Additional specimen examined. **New Zealand:** *South Island*: St Arnaud, 5 xii 1997, *J. Rowlands* (MEL).

We are greatly indebted to Dr David Galloway and to two anonymous referees who alerted us to the problems with the nomenclature of *M. bullata* and *P. stirtonii*, and assisted greatly in the clarification of this matter. We also extend many thanks to Professor Jack Elix for numerous HPLC analyses and for advice on chemistry, and to Dr Jean Jarman for assistance with the preparation of the figures. The generous support provided to G. K. by the Department of Botany, The Natural History Museum, London, is gratefully acknowledged. We also thank Dr Dagmar Triebel for the loan of specimens.

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