Studies on the lichen genus Cladia Nyl. in Tasmania: the C. aggregata Complex

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Abstract

The *Cladia aggregata* complex represents one of the most chemically and morphologically variable groups of lichens in southern Australasia, especially Tasmania. The complex is reviewed and eight species are recognised: the widespread *C. aggregata* (Sw.) Nyl., *C. inflata* (F. Wilson) D.J. Galloway and *C. schizopora* (Nyl.) Nyl.; and five species endemic to Tasmania: *C. deformis* Kantvilas & Elix *sp. nov., C. dumicola* Kantvilas & Elix *sp. nov., C. moniliformis* Kantvilas & Elix, *C. mutabilis* Kantvilas & Elix *sp. nov. and C. oreophila* Kantvilas & Elix *sp. nov.* The species are all characterised by a combination of habit, gross morphology, size of ascospores and conidia, and medullary chemistry. Within *C. aggregata* itself, six chemical races are identified: barbatic acid, fumarprotocetraric acid, stictic acid, psoromic acid, diffractaic acid and norstictic acid; the last two are not known to occur in Tasmanian species. A revised key to all thirteen species of *Cladia* Nyl. is provided.

Introduction

Cladia is primarily a southern Australasian lichen genus, with all of the nine species recognised by Filson (1992) occurring in that region. Of these, the most geographically restricted species are *C. ferdinandii*, which is found only in south-western Western Australia and southernmost South Australia, and *C. moniliformis*, which is endemic to south-western Tasmania. *Cladia fuliginosa* and *C. schizopora* also occur in South America, whilst *C. retipora* extends to New Caledonia. The most common and widespread species in the genus is *C. aggregata*, which has a southern circum-Pacific distribution, from Japan to Central America and the Caribbean, and also occurs in Madagascar and southern Africa.

In temperate regions of Australia, *C. aggregata* is found in virtually all vegetation types including coastal heathland, sclerophyll forest, rainforest, wet peatlands and alpine communities. It displays an often bewildering range of morphological and chemical variation and, in the past, numerous morphotypes have been accorded infra-specific rank (e.g. see Martin 1965). Galloway (1976) recognised one of the chemical-morphological variants as *C. inflata*, although Filson (1981) included this species within his concept of *C. aggregata* as a single, highly variable taxon. Kantvilas and Elix (1987) investigated the status of *C. inflata* and concluded that it was a distinct species, well separated from *C. aggregata* by morphology, chemistry and ascospore size. They also described a further, similarly distinguishable variant, *C. moniliformis*. Nevertheless, considerable variation remained within *C. aggregata* and *C. inflata* and further study of the morphology and chemistry of these species has revealed that they can be subdivided further. The results of these investigations are reported here.

The Cladia aggregata complex: overview of the problem

The *Cladia aggregata* group is characterised by having very fragile, hollow pseudopodetia, and apothecia which proliferate and form tiers (see Filson 1981 and Henssen 1981 for discussion). The pseudopodetia are typically some shade of olive-green or olive-brown. The group includes *C. aggregata*, *C. inflata*, *C. moniliformis* and *C. schizopora*, and the four new taxa described below: *C. deformis*, *C. dumicola*, *C. mutabilis* and *C. oreophila*.

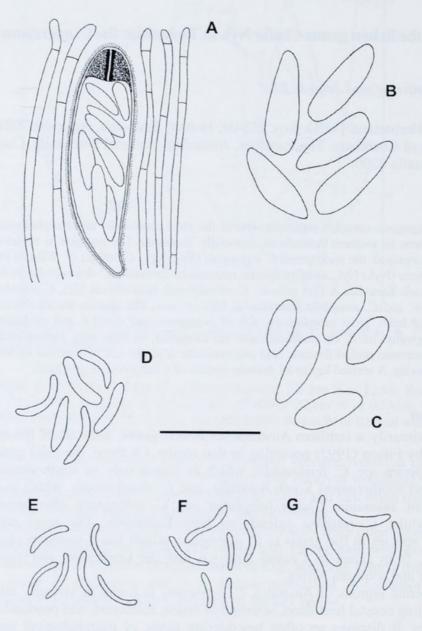


Fig. 1. Anatomy of *Cladia*: A asci, paraphyses and ascospores of *Cladia dumicola*, amyloid areas without pretreatment in KOH stippled; B ascospores of *C. moniliformis*; C ascospores of *C. deformis*; D conidia of *C. deformis*; E conidia of *C. inflata*; F conidia of *C. dumicola*; G conidia of *C. moniliformis*. Scale = 12 mm.

The key characters for separating the species within the group are the general habit of the thallus (erect or decumbent, clumped or dispersed, etc.), the shape and branching pattern of both the sterile and fertile pseudopodetia, including the form of their apices and axils, and the medullary chemistry. These and other characters of the species treated in this paper are summarised in Table 1. Initially, the size of the ascospores and conidia appeared to provide useful characters also, but large numbers of measurements served only to blur any size disjunctions between species. With the exception of *C. moniliformis*, the ascospores of the other taxa tend to fall within the range of $6-11 \times 2.5-4 \mu m$, and size differences are related mainly to the stage of development of the apothecia and asci rather than to the species involved. The same generally applies to conidia (Fig. 1).

Although the *C. aggregata* group is very widespread in the Southern Hemisphere and circum-Pacific regions, it is remarkable that most of the morphological and chemical variation is restricted to Tasmania. Five species (viz. *C. deformis, C. dumicola, C. moniliformis, C. mutabilis* and *C. oreophila*) are endemic to Tasmania, whilst

C. inflata occurs across southern Australasia but is most common in Tasmania. Even more remarkable is the fact that the endemic taxa (and much of the chemical variation) are confined to a very small region, namely the south-west, an area characterised by a flora rich in endemic angiosperms, gymnosperms and lichens (Kantvilas 1995).

At least some of the variability in the group is related to ecological factors. Thus inflated pseudopodetia tend to be found mostly in very wet habitats, with the most extreme form, the bulbous *C. moniliformis*, growing in the wettest, sometimes intermittently inundated, habitats, whereas the most slender forms of *C. aggregata* often occur in habitats most subject to drying out. Similarly, the water-repellant medullary compound, homosekikaic acid, is confined to *C. moniliformis*, the species most likely to be subjected to excessive hydration. Another hydrophobic compound, caperatic acid, is found only in *C. dumicola*, which occurs mainly in shaded habitats in very high rainfall areas. There remains the challenge to ascertain whether there is any adaptive significance in the distribution of the other chemical compounds.

The problem to be faced in the present project was to describe and partition the perplexing variation in a practical way. In past studies, such as on the genus Siphula, which shows a similar diversification in south-western Tasmania, chemistry provided a practical and unequivocal surrogate for interpreting the more subtle, morphological characters (Kantvilas 1996, 1998). Using this approach, we were alerted to the existence of C. moniliformis and C. deformis, two species easily recognised by morphological criteria also. However, limitations in the application of chemical characters were also encountered. Thus fumarprotocetraric acid, either alone or with its closely related derivatives, occurs virtually across the entire range of morphological variation exhibited by this species complex. Conversely, certain morphological types, such as the 'typical' C. aggregata form, span a wide range of chemotypes, such as those containing barbatic, fumarprotocetraric, stictic or psoromic acids. The approach of Filson (1981, 1992), where most of the variation in C. aggregata is encompassed within a single taxon, may be attractive for its convenience or simplicity. However, it is untenable in a region such as Tasmania, where it fails to account satisfactorily for the very obvious display of diversity in chemistry, morphology, anatomy and ecology, and of the links between these characters.

The present study is by no means a revision of the entire species complex, nor does it provide a solution to all the problems encountered. However, it identifies and segregates several well-defined entities in the group and attempts to summarise much of the variation as a basis for future studies.

Materials and methods

Work is based primarily on the first author's collections at HO, gathered in the course of extensive field studies, mainly in western Tasmania. Anatomical observations of asci and ascospores were made on apothecial sections and squashes mounted in water or Lugol's iodine after pretreatment with 10% KOH, or in ammoniacal erythrocin. The Lugol's is recommended in cases where there tend to be very few mature asci (e.g. in *C. inflata, C. mutabilis* or *C. deformis*); sections containing only sterile asci show little or no amyloid reaction and can, therefore, be readily identified as useless. Conidia were observed exclusively in ammoniacal erythrocin. Chemical analyses were undertaken using standard methods (Culberson 1972; Elix and Ernst-Russell 1993; Feige *et al.* 1993). Grid zones used in species distribution maps represent 10,000 metre intervals of the Australian Map Grid, Zone 55, Universal Transverse Mercator Projection; these have been widely used in Tasmania for presenting distributions of native species and plant communities (e.g. Williams and Potts 1996).

Table 1. Salie	Table 1. Salient features of species of the Cladia aggregata complex (the uniquely sorediate C. schizophora is omitted).	Cladia aggregata comp	olex (the uniquely sore	diate C. schizophora is o	mitted).		
	C. aggregata	C. deformis	C. dumicola	C. inflata	C. moniliformis	C. mutabilis	C. oreophila
Навіт	erect, ascending or decumbent, in clumps, tufts or swards	± erect in loose clumps	± erect in loose tufts or clumps	decumbent and interwoven in clumps or mats	decumbent, usually ± dispersed	erect, in clumps or swards	erect, in swards or clumps
STERILE PSEUDOPODETIA	OPODETIA						
Form	evenly cylindrical and tapered, occasionally inflated	unevenly inflated into irregular segments	not inflated, gradually tapering	inflated, ± evenly cylindrical	grossly inflated, with irregularly bulbous or cylindrical segments	slender and tapered or inflated, dimpled and puckered	inflated, unevenly cylindrical
Width	0.1–5 mm	1–7 mm	1–3 mm	1-4 mm	2-12 mm	0.4–5 mm	I-5 mm
Branching	repeatedly dichotomous or monopodial to sparsely dichotomous and with a main branch bearing short, stout laterals with deflexed apices	simple, or sparingly dichotomous at 15-45°	repeatedly dichoto- mous at <45°	repeatedly dichoto- mous at 35-90°	simple or sparsely irregularly branched, usually at >90°, sometimes lobulate	repeatedly di- or trichotomous at 20-45°	simple or sparsely dichotomous at 20-40°
Surface and colour	glossy and usually smooth, pale yellow- green, olive-brown, chestnut-brown to blackish brown	smooth, ± glossy olive-brown to reddish brown	smooth, glossy olive-green to olive- brown	smooth to wrinkled, ± glossy, yellow- olive- to reddish brown	smooth, becoming ±scabrid when old; yellow-brown to brown-black	smooth, ± glossy olive-brown to brown	matt, areolate, scabrid to bullate, pale grey to brownish
Axils	not perforate; not constricted	perforate or not, mostly constricted	not perforate; not constricted	not perforate, not constricted	not perforate, constricted	not perforate, not constricted	perforate, not constricted
Apices	mostly tapered and acute, or very abruptly tapered to truncate, with awl-like pycnidia	± rounded and blunt	acute to awl-like	truncate, with needle- like pycnidia	± rounded and blunt	acute to awl-like	abruptly tapered to a blunt point
Perforations	abundant	numerous	uncommon to abundant	few to absent	uncommon, often torn	numerous	absent to rare

Table 1. Continued

	C. aggregata	C. deformis	C. dumicola	C. inflata	C. moniliformis	C. mutabilis	C. oreophila
FERTILE PSEUDOPODETIA	OPODETIA						
Form	more robust and taller than sterile pseudopodetia	more slender and more perforate than sterile pseudopodetia	similar to sterile pseudopodetia but more perforate	identical to sterile pseudopodetia	more slender and more perforate than sterile pseudopodetia	more robust, more inflated and taller than sterile pseudopodetia	not known
Branching	racemose	corymbose	racemose	dichotomous	racemose	mostly corymbose	not known
ASCOSPORES	$(6-)7-11(-12) \times 2.5-4 \ \mu m$	$6-9 \times 2.5-4 \ \mu m$	$6.5{-}10\times2.5{-}4~\mu\mathrm{m}$	8-10 × 3-4 µm	$(8-)9-12 \times 3-4.5 \text{ µm}$	8–10 × 3–4.5 μm	not known
Conidia	5-8 × 0.6-1.5 µm	4.5-7 × 0.8-1.5 µm	$5-7 \times 0.6-1.5 \ \mu m$	$5-6 \times 0.6-0.8 \ \mu m$	$6-10 \times 0.6-1.5 \ \mu m$	(5-)6-8(-10) × 0.8- 1.5 μm	not known
CHEMISTRY	(a) barbatic, 4- <i>O</i> -demethyl- sti barbatic acids cr (b) fumarprotocetraric, m protocetraric (\pm), fu succinprotocetraric (\pm), pr physodalic (\pm) acids su (c) stictic, constictic, (\pm cryptostictic (\pm), norstictic (\pm), menegazziaic (\pm) acids (d) psoromic acid (f) diffractaic acid (f) diffractaic acid	stictic, constictic, cryptostictic (\pm) , menegazziaic (\pm) , fumarprotocetraric protocetraric (\pm) , succinprotocetraric (\pm) acids (\pm) ,	caperatic, norcaperatic (±), ursolic (±) acids	fumarprotocetraric, succinprotocetraric (±), protocetraric (±), physodalic (±) acids	homosekikaic, sekikaic (±) ramalinolic (±), 4'- <i>O</i> -methylnorhomo- sekikaic (±) acids	fumarprotocetraric acid	fumarprotocetraric acid

Generic characteristics

Cladia is characterised by a fruticose growth form, consisting of typically perforate pseudopodetia with an external cartilaginous layer. The apothecia are black or brown, with a prominent, persistent, proper margin and plane disc, eight-spored asci having a well-developed amyloid tholus with a darker staining central tube, stout, simple paraphyses and simple, hyaline ascospores (Fig. 1A). The pycnidia are immersed in glossy black to brown projections that are initially blunt and to *c*. 0.5 mm long, ultimately becoming needle-like or awl-like and to 1 mm long.

Following from the observations of Duvigneaud (1944), Galloway (1966) and Jahns (1972), Filson (1981) described a separate family, Cladiaceae, to accommodate the genus, chiefly on the basis of thallus and apothecial morphology. However, more commonly the genus is included in the Cladoniaceae (e.g. Hafellner 1988). Although it is not our intention to reassess the taxonomic position of *Cladia* here, it is significant that its ascus structure is of the typical *Cladonia*-type. Chemical composition in *Cladia* is also consistent with its inclusion in the Cladoniaceae.

Key to species of the genus Cladia

Fertile pseudopodetia to 1.5 cm tall, internally sorediate, intermingled with markedly shorter, squamule-like, sterile pseudopodetia with sorediate apices, or arising from a sorediate crust of crowded, reduced pseudopodetia; W.A., S.A., Vic., N.S.W., A.C.T., Tas., N.Z., South America
Pseudopodetia white to pale grey, occasionally in part faintly yellowish or pale brownish near the apices
Pseudopodetia with a compact, whitish inner medulla; perforations numerous and scattered, not forming a lace-like network; W.A., S.A., Q1d, N.S.W., A.C.T., Vic <i>C. corallaizon</i> F. Wilson ex Filson Pseudopodetia hollow or with a stranded inner medulla; perforations very numerous,
continuous and lace-like
Pseudopodetia with a compact, usually brown to black inner medulla
Cortex matt, crystalline, yellowish green to yellowish brown to blackened; W.A., N.S.W., Vic., Tas., N.Z., South America <i>C. sullivanii</i> (Müll. Arg.) W. Martin Cortex glossy, not crystalline, usually olive-brown to blackened; N.S.W., Vic., Tas., N.Z., South America <i>C. fuliginosa</i> Filson
Cortex matt, areolate, scabrid to bullate; Tas <i>C. oreophila</i> Kantvilas & Elix Cortex matt or glossy, smooth
Sterile pseudopodetia richly branched and tangled, forming spreading mats or cushions, very slender, mostly $0.5-1.5$ mm thick; fertile pseudopodetia markedly more robust, to <i>c</i> . 5 mm thick; very common, polymorphic, and widespread on soil, rocks, bark or wood

9.	Medulla Pd- (lacking fumarprotocetraric acid)	10
9.	Medulla Pd+ red (containing fumarprotocetraric acid)	12

- 10. Pseudopodetia grossly and irregularly inflated, with constricted axils and bulbous or cylindrical segments to 12 mm wide, typically rather decumbent and dispersed; containing homosekikaic acid; Tas.C. moniliformis Kantvilas & Elix
- 11. Sterile pseudopodetia ± monopodial, comprising ± erect main branches with short laterals with deflexed apices diverging at >45°; apices of main branches abruptly tapered to ± truncate; containing barbatic acid; widespread ...C. aggregata (Sw.) Nyl.
- Sterile and fertile pseudopodetia ± identical, decumbent, forming interwoven clumps or mats; perforations virtually absent, at least on the 'upper surface'; apices truncate; W.A., N.S.W., Tas., N.Z.
- 13. Sterile pseudopodetia with ± constricted axils, unevenly inflated segments and ± rounded, blunt apices; fertile pseudopodetia more slender than sterile pseudopodetia; containing stictic and fumarprotocetraric acids; Tas.....C. deformis Kantvilas & Elix
- 14. Sterile pseudopodetia inflated or, if not inflated, sparingly dichotomously branched to *c*. 1–3 times; fertile pseudopodetia corymbose; Tas.....*C. mutabilis* Kantvilas & Elix

Taxonomy

1. Cladia aggregata (Sw.) Nyl., Compt. Rend. Hebd. Séances Acad. Sci. 83: 88 (1876). Lichen aggregatus Sw., Prodr. 147 (1788). Type: Jamaica, O.P. Swartz. (lectotype, fide Filson 1981: S, n.v.).

For synonyms see Filson (1981).

Sterile pseudopodetia very variable, erect, ascending or decumbent, forming clumps, tufts or swards, decaying at the base, evenly cylindrical, most commonly not inflated and tapering to acute or awl-like apices, rarely inflated and then \pm truncate and tapering rather abruptly, (3–)10–80(–110) mm tall, (0.1–)0.5–1.5(–5) mm wide; surface pale yellow-green, green, olive or chestnut-brown to blackish brown, smooth and glossy, rarely somewhat dimpled, striate and chinky in older inflated thalli; branching rather variable, typically repeatedly dichotomous or rarely trichotomous, with branches densely entangled, or occasionally (in erect, inflated, alpine forms) monopodial, with a sparsely branched main axis bearing numerous short laterals; axils closed, not constricted, angles variable, with major branches diverging mostly at 45–90° but short laterals diverging at >90°; perforations very sparse to numerous, scattered or to one side of the pseudopodetia, slit-like to roundish or oval, (0.1–)0.5–3 mm wide; medullary cavity white, farinose.

Fertile pseudopodetia erect or, in epiphytic specimens, decumbent, typically more robust and taller than sterile pseudopodetia, mostly 1.5-3.5(-5) mm wide, 12-80 mm tall; branching racemose or occasionally ± corymbose; perforations abundant, 0.2-1.5 mm wide, sometimes forming a lace-like network in the upper part. *Apothecia* apical on short branchlets, 0.1-0.2 mm wide when well developed, proliferating in up to 6 tiers, clustered in groups of up to c. 12(-20). *Ascospores* ellipsoid, $(6-)7-11(-12) \times 2.5-4$ µm. *Pycnidia* common, at the apices of sterile pseudopodetia or on the lower laterals of fertile pseudopodetia. *Conidia* filiform to narrowly fusiform, straight or more commonly bent, $5-8 \times 0.6-1.5$ µm. (Fig. 2)

Chemistry: six chemical races are known and are treated separately below:

- (i) barbatic and 4-0-demethylbarbatic acids
- (ii) fumarprotocetraric, protocetraric (±), succinprotocetraric (±), physodalic acids (±)
- (iii) stictic, constictic, cryptostictic (±), norstictic (±), connorstictic and menegazziaic (±) acids
- (iv) psoromic acid
- (v) norstictic acid
- (vi) diffractaic acid (major), 4-0-demethyldiffractaic acid (minor).

Remarks: Cladia aggregata is an extremely variable species morphologically, and this variation is matched by its chemical diversity, wide ecological amplitude and extensive geographic distribution. The large number of taxonomic synonyms described for this species (Filson 1981) reflects this variability and the extent to which it has perplexed botanists in the past. It is significant that most of the variability is expressed only in Tasmania or in the southern Australasian region; further afield, *Cladia aggregata* is a relatively straightforward taxon with consistent chemical composition comprising barbatic acid. There is some confusion regarding the size of the spores of this species. Filson (1981, 1994) and other authors give these as $12-15 \mu m \log$, but we have not seen any spores longer than $12 \mu m$ and most are shorter than $10 \mu m$.

We have found no correlations between chemical composition and morphological, spore and conidial characters. Whilst there are many precedents for recognising the chemical races at infraspecific rank (as, for example, has occurred in several species of *Cladonia*), we have refrained from this course pending further study, but discuss the races separately below.

la. The barbatic acid race

This race represents *C. aggregata* in the strictest sense, and in its 'typical' form is characterised morphologically by highly branched and entangled, \pm cylindrical and evenly tapered, narrow, sterile pseudopodetia and markedly stouter, taller, erect, generally racemose fertile pseudopodetia. Sometimes it also occurs as a sward of fertile pseudopodetia. This race encompasses a fascinating range of morphologies. At one extreme are thalli with dark chestnut to blackish brown, very narrow, decumbent, sterile pseudopodetia, almost devoid of perforations; such forms are very similar to *Coelocaulon aculeatum* (Schreb.) Link (Parmeliaceae) and have been misidentified as such by many botanists, especially those unfamiliar with Australasian lichens. At the other extreme are very robust, \pm inflated, erect, scarcely branched, monopodial forms, found mostly in alpine habitats. In between there is a continuum of variation in thallus colour, branch thickness and growth form. Unlike the fumarprotocetraric acid-containing populations of *Cladia* where morphological disjunctions are discernible and underpin taxonomic entities, in our opinion, the barbatic acid race defies further subdivision.

Cladia aggregata in the strict sense is usually well separated from its relatives both chemically and morphologically. These other taxa have either bulbous, inflated (rather than cylindrical) fertile pseudopodetia, or sterile pseudopodetia quite unlike those of *C. aggregata*. Inflated forms of *C aggregata* (Fig. 2C) tend to be particularly distinctive

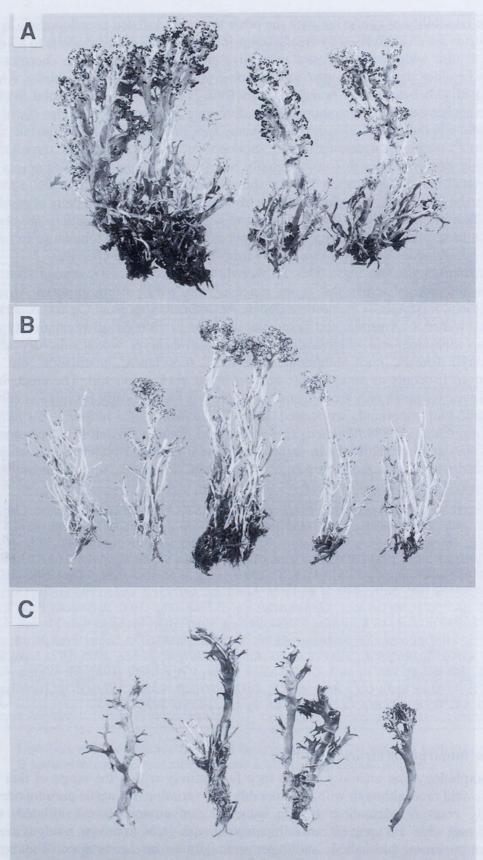


Fig. 2. Morphological variation in *Cladia aggregata*. A typical robust fertile pseudopodetia containing fumarprotocetraric acid (*Kantvilas 71/98*); B erect sterile and fertile pseudopodetia containing fumarprotocetraric acid (*Kantvilas 69/98*); C alpine, inflated form containing barbatic acid (*Kantvilas 162/86*). Scale in mm.

and the possibility of confusion with the other taxa with inflated pseudopodetia is slight. Such forms are characterised by erect, clump-forming sterile pseudopodetia to 80 mm tall and to 5 mm wide, with a glossy, pale olive-green to olive-brown to chestnut-brown cortex. In older thalli, the cortex may become striate or even rather chinky. Although occasionally dichotomously branching, this form is essentially monopodial, with erect main branches bearing stout, short laterals diverging at rather broad angles (from 50° to >90°) and tapering to awl-like, deflexed apices. The 'internodes' between the laterals may be up to 15 mm long, accentuating the 'monopodial' growth form. This very distinctive branching pattern makes this taxon readily recognisable in the field. The apices of the main branches tend to be tapered rather abruptly and are somewhat truncate (a little like those in the decumbent *C. inflata*), but are also terminated by about 4 pairs of needle-like or awl-like pycnidia. The axils are closed and not constricted, perforations are abundant and scattered, and the medullary cavity is persistently white and tomentose to farinose. Fertile pseudopodetia are very rare in this form but pycnidia are abundant.

Distribution and ecology: This is overwhelmingly the most common race of the species and occurs across the entire range of the genus, from southern Africa and Madagascar, East Asia as far north as Japan, Australasia, South and Central America and the West Indies. In Australia and Tasmania, it occurs in virtually all vegetation types and habitats, including arid rangelands, savannah-like eucalypt woodlands, dry and wet sclerophyll forests, cool temperate rainforest, moorlands, heathlands and alpine vegetation. It occurs as an epiphyte, and on wood, rock or on soil. The erect, inflated morphotype is known only from Tasmania where it is found mostly in alpine or subalpine heathland and moorland, associated with *C. sullivanii, C. retipora, C. fuliginosa C. inflata, Cladonia southlandica, C. murrayi* and *Siphula decumbens*. Occasionally it also occurs at lower altitudes in some buttongrass moorland communities where it is associated with *Cladia moniliformis, C. mutabilis, C. deformis, Siphula decumbens* and *S. jamesii.* (Fig. 3A)

Selected specimens examined (total = 217): AUSTRALIA, TASMANIA: near Collinsvale, $42^{\circ}51$ 'S, $147^{\circ}12$ 'E, *L. Rodway* s.n., May 1891 (HO); Deep Creek track, Mt Wellington, $42^{\circ}56$ 'S, $147^{\circ}14$ 'E, 480 m a.s.l., *W.A. Weymouth 639*, 23 Jan. 1899 (HO); Kingston, $42^{\circ}59$ 'S, $147^{\circ}18$ 'E, *W.M. Curtis* s.n., Apr. 1951 (HO); Mt Victoria Track, 880 m a.s.l., *G. Kantvilas* 51/81, 21 Feb. 1981 (BM, HO); The Clump, $41^{\circ}12$ 'S, $144^{\circ}52$ 'E, 150 m a.s.l., *A. Moscal* 4682, 9 Dec. 1983 (HO); The Knob, $42^{\circ}44$ 'S, $145^{\circ}58$ 'E, 440 m a.s.l., *G. Kantvilas* 191/95, 5 Dec. 1995 (HO); Dove Lake, $41^{\circ}40$ 'S, $145^{\circ}58$ 'E, 960 m a.s.l., *G. Kantvilas* s.n., 3 June 1986 (HO); Adamsons Peak, $43^{\circ}21$ 'S, $146^{\circ}49$ 'E, 930 m a.s.l., *G. Kantvilas* 162/86, 21 Sep. 1986 (HO); Mt Field West Plateau, $42^{\circ}49$ 'S, $146^{\circ}31$ 'E, 1400 m a.s.l., *G. Kantvilas* 44/80, 11 Mar. 1980 (HO); Scotts Peak Road near the airstrip, $43^{\circ}02$ 'S, $146^{\circ}19$ 'E, 340 m a.s.l., *G. Kantvilas* 77/80, 4 Apr. 1980 (HO); Mt Wedge, $42^{\circ}51$ 'S, $146^{\circ}18$ 'E, 1140 m a.s.l., *G. C. Bratt & F.N. Lakin* 71/1628, 4 Dec. 1971 (HO); Trevallyn SRA, $41^{\circ}27$ 'S, $147^{\circ}06$ 'E, 200 m a.s.l., *A.V. Ratkowsky* s.n., 12 Feb. 1992 (HO).

1b. The fumarprotocetraric acid race

The morphology and anatomy of this race fall entirely within the range of that of the barbatic acid race, although with considerably less variation. Its sterile pseudopodetia are typically erect or ascending, highly branched and entangled, not inflated, mostly 0.5-1.5 mm wide and up to 80 mm tall, pale yellowish green to brown, rarely if ever dark chestnut-brown or blackened, and taper gradually to an acute apex. The branches sometimes tend to diverge at rather acute angles ($c. 45^{\circ}$), whereas in the barbatic acid race most of the laterals diverge at angles of >90°. This subtle character is not consistent, however. As in the barbatic acid race, the fertile pseudopodetia are racemose, generally taller and more robust than the sterile pseudopodetia, and sometimes form extensive swards. This race never occurs as the blackened, decumbent, narrow-entangled

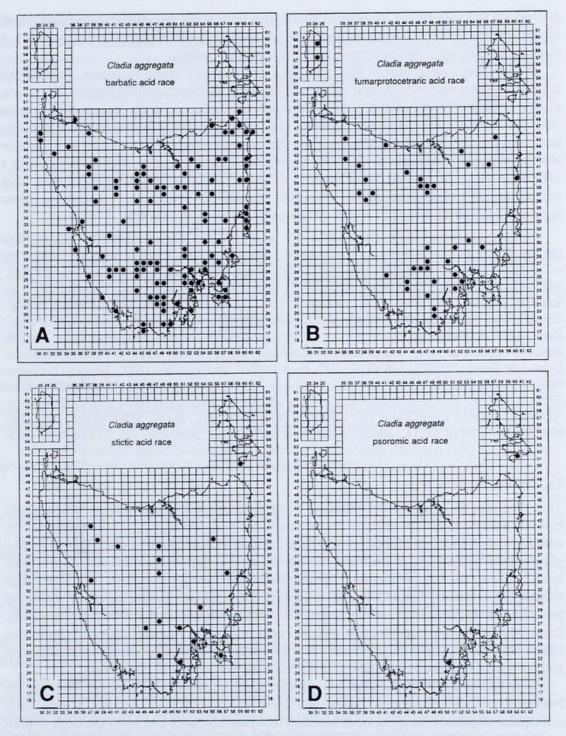


Fig. 3. Distribution of the chemical races of *Cladia aggregata* in Tasmania. A barbatic acid race;B fumarprotocetraric acid race; C stictic acid race; D psoromic acid race.

Coelocaulon-like form, nor as the erect, grossly inflated, monopodial forms.

Separation of this race of *C. aggregata* from other species of *Cladia* that contain fumarprotocetraric acid is usually straightforward. Only *C. inflata* consistently approaches it in branching pattern, but that species is recognised by the inflated sterile pseudopodetia, its usually decumbent habit, the virtual absence of perforations, and the morphology of the fertile pseudopodetia which are identical to the sterile ones. *Cladia deformis* and *C. oreophila* also differ from this race by having inflated pseudopodetia, the former also differing chemically, and the latter also having an areolate cortex. It is more difficult to

distinguish this race from *C. mutabilis* which may or may not be inflated; uninflated forms of that species differ by having very sparingly branched sterile pseudopodetia (usually 1-3 times instead of up to 6) and corymbose fertile pseudopodetia.

Distribution and ecology: This race is known mainly from Tasmania, with single collections from Antipodes Island and New Caledonia. Galloway (1985) implies that it may also be present in New Zealand, although this was not confirmed in the present study, whilst Ahti and Kashiwadani (1984) and Stenroos *et al.* (1992) record it from southern Chile. The latter authors also record a race comprising fumarprotocetraric acid together with barbatic acid, an unusual combination which we have never observed in our studies. It grows in a very wide range of habitats from lowland to alpine altitudes, in sclerophyll forest, cool temperate rainforest, buttongrass moorland, heathland and alpine vegetation. Most specimens are terricolous, but it also occurs on wood or as an epiphyte. (Fig. 3B)

Selected specimens examined (total = 47): AUSTRALIA, TASMANIA: Mt Wellington, The Springs, 720 m a.s.l., *R.D. Seppelt 19310*, 18 Feb. 1994 (HO); Liffey Bluff, 41°43'S, 146°47'E, 900 m a.s.l., *A. Moscal 17704*, 23 Apr. 1989 (HO); Scotts Peak Road near the airstrip, 43°02'S, 146°19'E, 340 m a.s.l., *G. Kantvilas 102/95*, 21 Sept. 1995 (HO); King Island, Pegarah Forestry Reserve, 39°56'S, 144°00'E, *I.D. Cameron* s.n., 13. June 1965 (HO); near Dunrobin Bridge, 42°32'S, 146°44'E, *G.C. Bratt 67/48*, 30 July 1967 (HO); Savage River Pipeline, south of Rapid River, 41°16'S, 145°19'E, 480 m a.s.l., *G. Kantvilas 728/80*, 27 Nov. 1980 (BM, HO); Anthony Road, 41°49'S, 145°38'E, 450 m a.s.l., *G. Kantvilas 164/97*, 6 May 1997 (HO); continuation of Lonnavale Road, 42°58'S, 146°48'E, *G.C. Bratt 69/818*, 26 Oct. 1969 (HO); Mother Cummings Peak, 41°40'S, 146°32'E, 850 m a.s.l., *A. Moscal 12347*, 20 Feb. 1986 (HO); Adamsons Peak, 43°21'S, 146°49'E, 930 m a.s.l., *G. Kantvilas 163/86*, 21 Sep. 1986 (HO). NEW ZEALAND, ANTIPODES ISLAND: south side of Hut Cove, [75–90 m a.s.l.], *R.C. Harris 5820*, 16 Feb. 1970 (HO, MSC). NEW CALEDONIA: summit of Mt Bouo, 1050 m a.s.l., *B.M. Potts* s.n., 21 Feb. 1991 (HO).

1c. The stictic acid race

This race also falls within the range of morphological and anatomical variation of the barbatic acid race. In most specimens, the sterile pseudopodetia are typically rather narrow and 0.4-1 mm wide, uninflated, evenly tapered, pale yellow-green to chestnut-brown and glossy. Whilst some are \pm erect and have acute-angled axils, others are decumbent with broadly divergent lateral branches. Some sterile specimens, especially ones from high altitudes, are rather distinctive and resemble *C. dumicola*, having sparsely branched pseudopodetia. These may well represent a distinct taxon, but on the collections available, it has been difficult to circumscribe such an entity other than by using chemical characters. Stictic acid also occurs in *C. deformis*, which in addition contains fumarprotocetraric acid and has grossly inflated pseudopodetia with constricted axils and internodes.

Distribution and ecology: This uncommon race is known from Tasmania, Victoria, the Furneaux Islands, Macquarie Island and New Zealand. It too displays a very wide ecological amplitude, ranging from lowland to alpine altitudes and from the high rainfall areas of western Tasmania to the drier parts of the east. All collections are from soil in open habitats in moorland and heathland. (Fig. 3C)

Selected specimens examined (total = 21): AUSTRALIA, TASMANIA: south of Que River, 41°35'S, 145°40'E, 650 m a.s.l., *G. Kantvilas* s.n., 22 May 1986 (HO); Lake Dove, 41°40'S, 145°58'E, *G. Kantvilas* s.n., 3 June 1986 (HO); track to Beatties Tarn, 42°41'S, 146°39'E, 920 m a.s.l., *G.C. Bratt & J.A. Cashin 421*, 18 Aug. 1963 (HO); 2 km west of New Norfolk, 42°47'S, 147°02'E, 90 m a.s.l., *G. Kantvilas* s.n., 19 Feb. 1997 (HO); Mount Koonya, 43°06'S, 147°48'E, 300 m a.s.l., *A. Moscal 5211*, 1 Jan. 1984 (HO); Bass Strait, Clarke Island, 55 m a.s.l., *J.S. Whinray 1513*, 30 June 1981 (HO, MEL). VICTORIA: Great Western, 37°09'S, 142°52'E, *G.C. Bratt 67/119*, 30 Sep. 1967 (HO). NEW ZEALAND: Foggy Peak, 43°17'S, 171°45'E, *G.C. Bratt 72/1897*, 12 Nov. 1972 (HO). MACQUARIE ISLAND: Razor Back Ridge, 54°34'S, 158°57'E, *R.D. Seppelt 15402*, 11 Feb. 1985 (HO).

1d. The psoromic acid race

This very rare chemotype is known only from two, small, fragmented specimens from gritty, quartzitic soil in lowland heathland. Both have sterile pseudopodetia which are decumbent, only 0.3–0.5 mm wide, glossy chestnut-brown, taper evenly to a point, and are sparsely branched with axillary angles ranging from acute to obtuse. Well-developed fertile pseudopodetia have not been seen, but the few spores observed are 8–10 × 3 μ m and thus identical with those of the other races of *C. aggregata*. (Fig. 3D)

Specimens examined: AUSTRALIA, TASMANIA: Randalls Bay, 43°15'S, 147°08'E, G.C. Bratt & K.M. Mackay 69/407, 18 May 1969 (HO); Bass Strait, Clarke Island, 46 m a.s.l., J.S. Whinray 1402, 24 Mar. 1980 (HO, MEL).

1e. The norstictic acid race

This rare chemotype is known from a single collection from arid south-western Western Australia where it grew on soil. It has a *Coelocaulon*-type morphology of brown, narrow, entangled sterile pseudopodetia with broadly diverging branches.

Specimen examined: AUSTRALIA, WESTERN AUSTRALIA: Kondinin Forestry Reserve, 32°30'S, 118°24'E, 300 m a.s.l., G.C.Bratt 67/367 (HO).

1f. The diffractaic acid race

This rare chemotype is known from a single collection from sandstone in open eucalypt woodland in New South Wales. It was not available for study.

Specimen examined: AUSTRALIA, New SOUTH WALES: Morton National Park, 8 km NE of Nerriga, 35°07'S, 150°08'E, J.A. Elix 5089, 31 Oct. 1978 (MEL).

2. Cladia deformis Kantvilas & Elix sp. nov.

Species *Cladiae moniliformi* aliquantum similis, pseudopodetiis sterilibus valde inflatis et axillis constrictis, sed acidum sticticum et acidum fumarprotocetraricum continens, habitu erectiore fasciculatoque et segmentis elongatioribus.

Type: Tasmania, Scotts Peak Road near airstrip, 43°02'S, 146°19'E, on wet peaty soil in buttongrass moorland, 340 m a.s.l., 8 Mar. 1991, *G. Kantvilas* 87/91 (holotype HO).

Sterile pseudopodetia ± erect, forming loose clumps, decaying at the base, unevenly inflated, puckered and dimpled, and somewhat constricted into irregular, elongate segments, 35-50 mm tall, (1-)2-5(-7) mm wide, simple or sparingly dichotomously branched, generally with apices ± rounded and blunt, or with occasional awl-like pycnidia; surface smooth to slightly wrinkled in older parts, often rather glossy, typically olive-brown to reddish brown, tending to pale olive-greenish in shade, blackened near the base; axils of main branches open or closed, forming angles of 15-45° (occasional short laterals diverging at up to 90°), generally \pm constricted; perforations 0.3–3 mm wide, usually numerous, roundish to oval, sometimes torn, often mainly towards one side of the pseudopodetia; medullary cavity farinose, white, or brownish where exposed. Fertile pseudopodetia not common, similar in size and form to sterile pseudopodetia, or somewhat more slender, typically more perforate and corymbose towards the apices, ± discrete or arising as laterals from sterile pseudopodetia. Apothecia apical, 0.1-0.2 mm wide, glossy, with a dark red-brown proper margin and black disc, typically clustered in loose groups of 2-7(-9), single or two-tiered. Ascospores ellipsoid or tapered somewhat at one end, 6-9 × 2.5-4 µm. Pycnidia occasional, usually single on short lateral branches, at the apices of main branches of sterile pseudopodetia or, rarely, on fertile

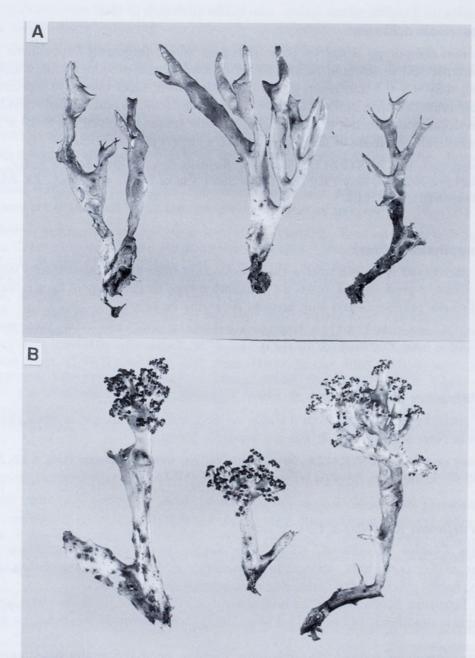


Fig. 4. *Cladia deformis (Kantvilas 70/98).* A sterile pseudopodetia; B fertile pseudopodetia. Scale in mm.

pseudopodetia. *Conidia* fusiform to filiform, with blunt apices, straight, sigmoid or curved, $4.5-7 \times 0.8-1.5 \mu m$. (Figs 1C–D, 4)

Chemistry: stictic acid, constictic acid, cryptostictic acid (\pm), menegazziaic acid (\pm), fumarprotocetraric acid, succinprotocetraric acid (\pm), protocetraric acid (\pm); medulla Pd+ red, K-, KC-, C-, UV-.

Remarks: *Cladia deformis* is characterised unequivocally by the combination of a grossly inflated thallus and the presence of stictic acid in the medulla. However, the concentration of this compound is not sufficiently high to be detectable with certainty by means of a spot test with KOH. Indeed in one specimen, which on the basis of morphology alone clearly belonged to *C. deformis*, we were able to detect stictic acid only in the very apices of the pseudopodetia but nowhere else in the thallus.

The new species is rather variable and its morphology may overlap to some extent that of other related species. Its constricted axils and semi-constricted, unevenly 'segmented' internodes ally it most closely with *C. moniliformis*. However, in addition to containing homosekikaic acid, *C. moniliformis* differs in having much more bulbous pseudopodetial segments (in *C. deformis* they are unevenly elongate), and a dispersed, prostrate habit. In contrast, *C. deformis* tends to form semi-erect clumps. The two species also differ somewhat in their colour and surface texture: *C. deformis* tends to be a glossy reddish brown, whereas *C. moniliformis* is yellow-brown to blackened, and matt at least in older

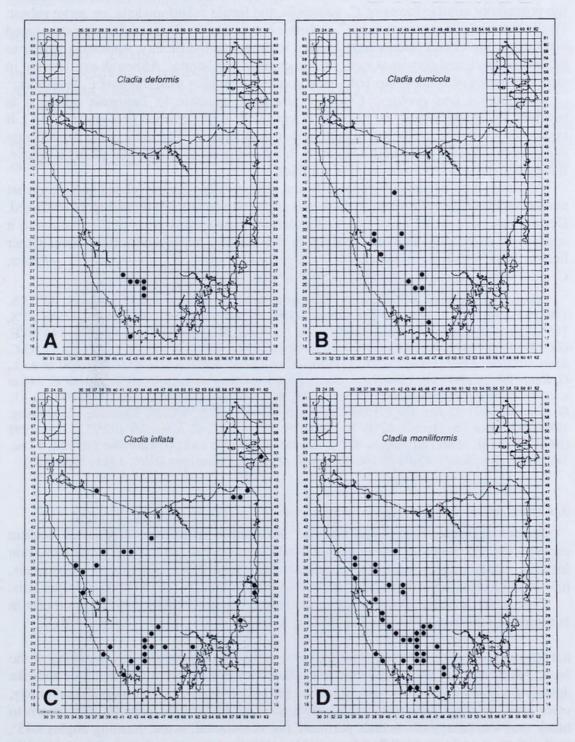


Fig. 5. Distribution of species of *Cladia* in Tasmania. A *C. deformis*; B *C. dumicola*; C *C. inflata*; D *C. moniliformis*.

parts of the thallus. When fertile, *C. deformis* is distinguishable from *C. moniliformis* by the generally more robust and essentially corymbose fertile pseudopodetia (in *C. moniliformis* these are quite slender and rather racemosely branched) and by its smaller spores.

Also potentially similar are some of the forms of *C. mutabilis*, which may also have grossly inflated, rather bulbous pseudopodetia. In this case, these two taxa can be separated morphologically, in that the sterile pseudopodetia of *C. deformis* tend to have blunt to \pm rounded apices whereas those of *C. mutabilis* may be rather pointed and tapered. *Cladia deformis* also tends to have larger, more prominent perforations. Its fertile pseudopodetia are usually rather slender in comparison with the sterile ones, whereas in the potentially similar forms of *C. mutabilis*, the fertile pseudopodetia are more robust. Fertile material is not common in *C. deformis* but, unlike in *C. mutabilis*, well developed asci containing mature spores were located without much difficulty. Apothecia appear to be rarely tiered, and consist at most of two compressed 'strata'. Although overlapping in size, the spores of *C. deformis* tend to be somewhat smaller than those of *C. mutabilis*.

Distribution and ecology: Cladia deformis is endemic to Tasmania where it is confined to the south-west, exclusively to areas with a Precambrian geology (Fig. 5A). It occurs on peaty or gravelly soil in buttongrass moorland, usually in the most depauperate sites where drainage is poorest, the soil is thin and the cover of vascular plants is sparse. It ranges from sea-level to subalpine altitudes.

Although it co-occurs geographically and ecologically with the related and somewhat similar species *C. moniliformis*, *C. deformis* appears to be much rarer and more restricted. Despite extensive sampling of *Cladia* populations across many areas of the southwest, it appears to be locally abundant mainly in the Gordon River-Scotts Peak area. Other lichens with which it is associated include *Cladia inflata*, *C. aggregata*, *C. retipora*, *C. sullivanii*, *Cladonia southlandica*, *Siphula jamesii* and *S. decumbens*.

Specimens examined: AUSTRALIA, TASMANIA: Scotts Peak Road near Clear Creek, 42°53'S, 146°23'E, 360 m a.s.l., *G. Kantvilas 99/95*, *100/95*, 21 Sep. 1995 (HO); Wilsons Bight, 43°32'S, 146°05'E, 30 m a.s.l., *A.M. Buchanan 9421*,13 Jan. 1987 (HO); Edgar Lake, 43°01'S, 146°20'E, *G.C. Bratt et al. 70/1200*, 11 Oct. 1970 (HO); Wedge River, 42°51'S, 146°14'E, 360 m a.s.l., *G.C. Bratt 68/220a*, 15 Mar. 1968 (HO); Condominium Creek, 42°57.5'S, 146°21.5'E, 360 m a.s.l., *G. Kantvilas* s.n., 28 Aug. 1986 (HO); Scotts Peak Road near airstrip, 43°02'S, 146°19'E, 340 m a.s.l., *G. Kantvilas* 104/95, *105/95*, 21Sep. 1995 (HO); Mt Sprent, 42°48'S, 145°58'E, 700 m a.s.l., *G. Kantvilas* s.n., 31 Jan. 1987 (HO); The Knob, 42°44'S, 145°58'E, *G. Kantvilas* s.n., 28 Aug. 1986 (HO); near The Hermit, 42°49'S, 146°08'E, 320 m a.s.l., *G. Kantvilas* 192/95, 5 Dec. 1995 (HO); 1.5 km SE of McPartlan Pass, 42°52'S, 146°12'E, 330 m a.s.l., *G. Kantvilas* 195/95A, 5 Dec. 1995 (HO); Red Knoll, 43°02'S, 146°17'E, 440 m a.s.l., *G. Kantvilas* 70/98, 3 Feb. 1998 (HO).

3. Cladia dumicola Kantvilas & Elix sp. nov.

Species *Cladiae aggregatae Cladiae inflataeque* manifeste affinis sed acidum caperaticum continens et pseudopodetiis nitidis olivaceis, comparate gracilibus, non inflatis, acutangulatis ramosis, concinne decrescentibus, ascosporis ellipsoideis, 6.5–10 µm longis, 2.5–3.5 µm latis, et conidiis filiformibus, 5–6.5 µm longis, 0.6 µm latis.

Type: AUSTRALIA, TASMANIA, Condominium Creek, 42°58'S, 146°22'E, on peat in buttongrass moorland, 330 m a.s.l., 28 Aug. 1986, *G. Kantvilas* s.n. (holotype HO).

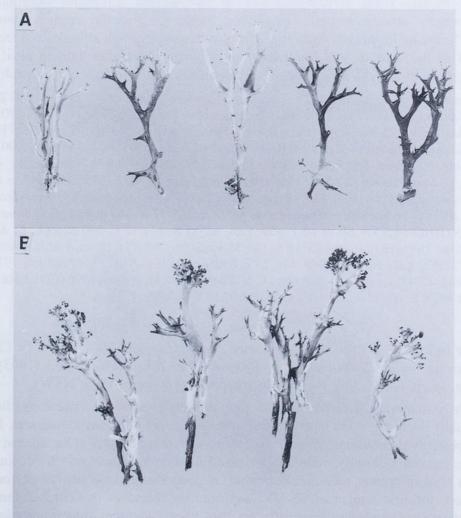
Sterile pseudopodetia \pm erect, forming loose tufts or compact clumps, decaying at the base, 30–60 mm tall, 1–3 mm wide, not inflated, tapered gradually to acute or awl-like apices, \pm regularly dichotomously branched (up to *c*. 6 times); surface smooth and glossy, olive-green to olive-yellow, to olive-brown in exposed habitats, usually dark brown to black near the base; axils neither perforate nor constricted, acute, forming angles <45°, perforations round to oval, 0.2–1.5 mm wide, uncommon, scattered or abundant, but then usually concentrated in a single rank along one side of the pseudopodetia or near their

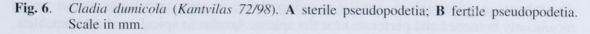
apices; medullary cavity white and tomentose throughout. *Fertile pseudopodetia* similar in size and form to sterile pseudopodetia, except usually more densely branched near the apices and with more abundant perforations, racemose. *Apothecia* apical, to 0.2 mm wide, black and glossy, with a prominent, persistent proper margin and plane, \pm sunken disc, occurring singly or in clusters of 2–5 per branch, occasionally proliferating in rather compressed tiers. *Ascospores* ellipsoid, $6.5-10 \times 2.5-4 \mu m$. *Pycnidia* common, occurring singly or in pairs, mostly at the apices of sterile pseudopodetia or, occasionally, amongst the apothecia on fertile pseudopodetia. *Conidia* filiform, with blunt apices, straight or curved, $5-7 \times 0.6-1.5 \mu m$. (Figs 1A, 1F, 6)

Chemistry: caperatic acid, norcaperatic acid (±), ursolic acid (±); medulla K-, Pd-, KC-, C-, UV-.

Remarks: Cladia dumicola is a very distinctive species, characterised morphologically by its relatively slender, elongate, glossy olive-coloured pseudopodetia. As with most *Cladia* species, medullary chemistry is a critical aid to identification and, in this case, *C. dumicola* is unique in the *C. aggregata* complex in containing fatty acids.

Although previously included by us within a rather broad concept of *C. inflata* (Kantvilas and Elix 1987), the new species has pseudopodetia which, although at times rather robust, are not markedly inflated, but are relatively neatly tapered and cylindrical.





It is most similar morphologically to some forms of *C. mutabilis*, which have sparsely branched, sometimes quite slender pseudopodetia with acute-angled axils. These forms, however, differ chemically in containing fumarprotocetraric acid; they also tend to be much shorter.

Fertile pseudopodetia are not uncommon in this species and, furthermore, most apothecia studied were well-formed and with abundant, well-developed asci containing spores. This is in sharp contrast to material studied of *C*.'*inflata* and *C. mutabilis* where most apothecia seem to lack fertile asci. The fertile pseudopodetia are not unlike those of *C. aggregata* although they are more loosely branched and not significantly more robust than the sterile ones. Tiered, proliferating apothecia are uncommon in *C. dumicola*, in contrast to other species of this complex. The abundant occurrence of pycnidia and apothecia together on the same supporting branchlet appears to be unusual; in other species of the *C. aggregata* group, the development of pycnidia is confined mainly to sterile pseudopodetia.

Distribution and ecology: Cladia dumicola is endemic to Tasmania where it is confined to western and south-western regions (Fig. 5B). Although typically associated with other species of Cladia, viz. C. aggregata, C. inflata, C. retipora and C. sullivanii, it appears to have a narrower ecological range than these widespread relatives. It has been recorded mostly from scrubby copses in buttongrass moorland dominated by Leptospermum, Melaleuca and Agastachys, hence the specific epithet 'dumicola', meaning 'growing in shrubby thickets'. It is also frequent in high altitude cool temperate rainforest of the thamnic and implicate type (nomenclature after Jarman et al. 1994) where it grows in well-lit sites on the forest floor, associated mainly with bryophytes.

Specimens examined: AUSTRALIA, TASMANIA: Algonkian Mountain, 42°24'S, 146°03'E, 950 m a.s.l., *G. Kantvilas 64/90*, 7 Mar. 1990 (HO); Eastern Arthur Range, 43°14'S, 146°26'E, 780 m a.s.l., *G. Kantvilas 119/91*, 25 Mar. 1991 (HO); north of Precipitous Bluff, 43°25.5'S, 146°36.5'E, 730 m a.s.l., *G. Kantvilas 116/90*, 14 Mar. 1990 (HO); Weindorfers Forest, 41°38'S, 145°56'E, 900 m a.s.l., *G. Kantvilas, B. Fuhrer, S.J. Jarman 13/92*, 25 Jan. 1992 (HO); King William Saddle, 42°13'S, 146°06'E, *G. Kantvilas* s.n., 27 Sep. 1986 (HO); Dove Lake, 41°40'S, 145°58'E, 940 m a.s.l., *G. Kantvilas* s.n., 3 June 1986 (HO); Elliot Range, 42°28'S, 145°43'E, 880 m a.s.l., *G. Kantvilas* s.n., 12 Jan. 1985 (HO); *c.* 26 km SSE of Queenstown, 42°18'S, 145°37'E, 280 m a.s.l., *G. C. Bratt 71/981*, 14 June 1971(HO); 1.5 km SE of McPartlan Pass, 42°52'S, 146°12'E, 330 m a.s.l., *G. Kantvilas* 196/95, 5 Dec. 1995 (HO); Crotty, 42°12'S, 145°38'E, 200 m a.s.l., *G.C. Bratt & M.H. Bratt 72/113*, 1 Apr. 1972 (HO); Lake Judd, 42°59'S, 146°25'E, 640 m a.s.l., *G.C. Bratt 73/908*, 28 July 1973 (HO); Gordon Road, 42°47'S, 146°24'E, 480 m a.s.l., *G. Kantvilas 80/96*, 10 Nov. 1996 (HO); Lake Sydney, 43°17'S, 146°36'E, 680 m a.s.l., *G. Kantvilas 64/98*,14 Mar. 1998 (HO).

4. *Cladia inflata* (F. Wilson) D.J. Galloway, *Nova Hedwigia* 28: 476 (1977). *Cladonia aggregata* var. *inflata* F. Wilson, *Pap. Proc. R. Soc. Tasm.* (1892): 153 (1893). *Type*: Tasmania, Maria Island, *R.A. Bastow* (lectotype *fide* Galloway 1977, NSW).

Sterile pseudopodetia decumbent, forming densely interwoven, spreading clumps or mats, usually decaying at the base, to 50 mm long, \pm evenly inflated-cylindrical, 1–4 mm wide, repeatedly dichotomously branched, tapering rather abruptly at the apices; surface \pm glossy, smooth to faintly undulate, wrinkled or dimpled, pale yellow-brown, olive-brown to reddish brown, pale greenish when in deep shade; axils neither perforate nor constricted, forming angles of 35–90°; perforations round to oval, 0.2–2 mm wide, usually very few to absent, especially on the 'upper' surface, sometimes numerous; medullary cavity white tomentose throughout. *Fertile pseudopodetia* uncommon, decumbent, \pm identical to sterile pseudopodetia, except sometimes rather more racemosely branched and perforate near the apices. *Apothecia* apical on short branchlets,

mostly solitary or in groups of 2–3, to 0.2 mm wide, usually proliferating in 2–3 compressed tiers, typically sterile and comprised internally of erect, stout, sterile hyphae and very deformed, weakly amyloid or non amyloid asci. *Ascospores* very rare, ellipsoid, $8-10 \times 3-4 \mu m$. *Pycnidia* common, occurring singly or in pairs at the apices of the sterile and fertile pseudopodetia, occasionally also laminal. *Conidia* filiform, falcate, with blunt apices, $5-6 \times 0.6-0.8 \mu m$. (Figs 1 E, 7)

Chemistry: fumarprotocetraric acid, succinprotocetraric acid (\pm) , protocetraric acid (\pm) , physodalic acid (\pm) ; medulla K-, KC-, C-, Pd+ red, UV-.

Remarks: The above description pertains to what we define here as *Cladia inflata* in the strict sense. This distinctive taxon is characterised by its decumbent, clump or mat-forming habit, and by its pseudopodetia which are broad and rather regularly inflated and cylindrical, and repeatedly dichotomously branched, usually at rather wide angles (up to 90°). Also very distinctive are the apices of the pseudopodetia which taper very abruptly before terminating in pycnidia, and hence appear rather truncate; in contrast, the

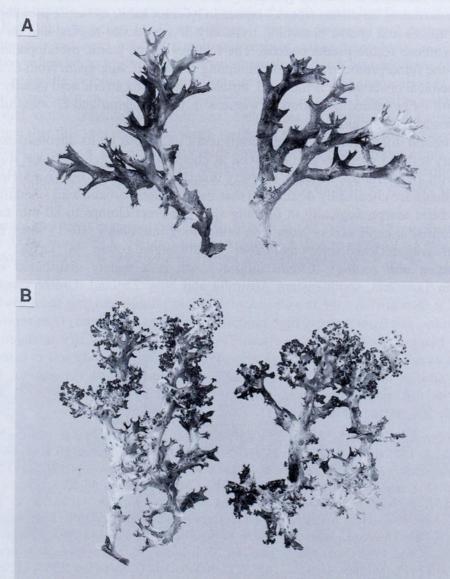


Fig. 7. Cladia inflata (Kantvilas 73/98). A sterile pseudopodetia; B fertile pseudopodetia. Scale in mm.

pseudopodetia of the other species of the group taper gradually to a point or are blunt and rounded. In typical specimens, perforations are very few and often none at all are evident when the thallus is viewed from above. Fertile pseudopodetia are uncommon, but are \pm identical with the sterile pseudopodetia in form and size. Despite studying numerous, seemingly well-developed apothecia, fertile asci or spores appear to be rare. The 'hymenium' instead contains mostly numerous, robust, erect sterile hyphae and occasional deformed or immature asci which do not display the expected amyloid reactions.

The type specimen of *C. inflata* is rather fragmented and small, but nevertheless clearly displays the characteristic morphology of this species. It contains fumarprotocetraric acid, succinprotocetraric acid (trace), protocetraric acid (trace) and physodalic acid (minor). Its provenance (Maria Island, eastern Tasmania) is also well within the known distribution of *C. inflata* as defined by us.

In our view, *C. inflata* is easily recognised in the field, especially when welldeveloped. Perhaps the most similar species is *C. mutabilis*, and indeed, the decision to segregate the latter as a separate taxon was taken only after a very extensive study of a wide range of material, both in the laboratory and the field (see also under *C. mutabilis*, below). *Cladia mutabilis* differs from *C. inflata* in its erect habit, its sterile pseudopodetia with acute apices and sparse branching, typically at very acute angles, and its robust, mainly corymbose fertile pseudopodetia. The features of the sterile pseudopodetia also distinguish the fumarprotocetraric acid-containing races of *C. aggregata* from *C. inflata*. A minor chemical observation is that in *C. inflata*, fumarprotocetraric acid usually occurs together with other related compounds, whereas in *C. aggregata* and *C. mutabilis*, this substance tends to occur alone.

Cladia inflata differs from *C. moniliformis* and *C. deformis* by its unconstricted axils and regularly inflated pseudopodetia, as well as chemically. At high altitudes, it may be confused with a very robust, inflated, sparsely branched form of *C. aggregata*. However, such individuals are chemically distinct, in that they contain barbatic acid (medulla Pd-). They also differ morphologically in forming sparse \pm erect clumps to 80 mm tall, and usually comprise a main axis or axes with rather long internodes (10–15 mm), bearing short laterals with deflexed apices and rather broadly angled (often >90°) axils.

Distribution and ecology: Cladia inflata s. str. is a widely distributed species, occurring in Tasmania, south-eastern Australia and New Zealand. Unlike most of its segregates, it also displays the broadest ecological amplitude, ranging from lowland to alpine altitudes, and from the very high rainfall (>3000 mm per annum) Gymnoschoenus-dominated blanket bogs of south-western Tasmania to relatively dry heathlands and sclerophyll woodlands (Fig. 5C). It typically grows on peaty or sandy soil in association with other species of Cladia, Cladonia southlandica and Siphula decumbens. Further details of its distribution are given for New Zealand by Galloway (1977) and for Tasmania by Kantvilas and Elix (1987).

Selected specimens examined (total = 35): AUSTRALIA, NEW SOUTH WALES: Morton National Park, 35° 07' S, 150° 08' E, 760 m a.s.l., J.A. Elix 19281 & J. Johnston, 26 June 1985 (HO, distributed as Lichenes Australasici Exsiccati 102). TASMANIA: Mt Cameron, 40°59'S, 147°57'E, c. 500 m a.s.l., G. Kantvilas 81/93, 13 Aug. 1993 (HO); Mt Wellington, 42°55'S, 147°14'E, A.V. Ratkowsky L71, 12 Nov. 1980 (BM, HO); summit of Moores Pimple, 41°52'S, 145°29'E, L. Rodway s.n., Nov. 1893 (HO); plateau south of Mt Darwin, 42°17'S, 145°35'E, 680 m a.s.l., G.C. Bratt & J.A. Cashin 71/936, 12 June 1971 (HO); Rocky Cape, 40°51'S, 145°30'E, 270 m a.s.l., G. Kantvilas s.n., 5 June 1986 (HO); Mt William, 40°55'S, 148°11'E, 120 m a.s.l., A. Moscal 2541, 8 Sep. 1983 (HO); Flynns Tarn, 41°41'S, 145°58'E, 960 m a.s.l., G. Kantvilas 93/95, 17 Sep. 1995 (HO); Mt Norold, 43°15'S, 146°15'E, 950 m a.s.l., G. Kantvilas 33/94, 24 Feb. 1994 (HO); Red Knoll, 43°02'S, 146°17'E, 440 m a.s.l., G. Kantvilas 95/95, 21 Sep. 1995 (HO); Lawson Range, 42°57'S, 145°41'E, 520 m a.s.l., A. Moscal 11911, 24 Jan. 1986 (HO); Bass Strait, Cape Barren Island, c. 250 m a.s.l., J.S. Whinray 1251, 20 Apr. 1980 (HO, MEL).

5. *Cladia moniliformis* Kantvilas & Elix, *Mycotaxon* 29: 199 (1987). *Type:* Australia, Tasmania, north of Sentinel Range, *c*. 4 km SE of Mt Cullen, on wet peaty soil in buttongrass moorland, 320 m a.s.l., 2 Nov. 1986, *G. Kantvilas & J. Jarman 169/86* (holotype HO; isotypes BM, CANB, MEL 2051773).

A full description of this species is given by Kantvilas and Elix (1987) and is not repeated here. *Cladia moniliformis* is characterised by a dispersed to decumbent habit, grossly inflated sterile pseudopodetia with markedly constricted axils and irregularly bulbous or cylindrical segments to 12 mm wide, and by its rather slender, racemose fertile pseudopodetia. Since our earlier work (Kantvilas and Elix 1987), we have also revised the observed dimensions of the spores and conidia: spores are $9-12 \times 3-4.5 \mu m$, (marginally larger than those of the other species in the group) whereas the conidia are $6-10 \times 0.6-1.5 \mu m$ (also marginally longer) (Figs 1B, 1G). *Cladia moniliformis* is chemically unique in the genus and contains homosekikaic acid (medulla K-, KC-, C-, UV-, Pd-) (see also Table 1).

When well developed, *C. moniliformis* is one of the easiest members of this species complex to recognise in the field. The most superficially similar species is *C. deformis* and, where the two taxa occur together, considerable care must be taken in distinguishing them. Key field characters for *C. moniliformis* are the dispersed and decumbent, rather than clumped and erect habit, the matt and scabrid rather than glossy surface of older thalli, the yellowish to blackish rather than somewhat reddish brown colour of the cortex, and the generally bulbous rather than elongate pseudopodetial segments (Fig. 8).

The distribution and ecology of the species is discussed by Kantvilas and Elix (1987). Since that work, considerable additional field work in Tasmania and elsewhere has confirmed that this species is very much restricted to the south-west of Tasmania, where it is found mostly on gravelly, peaty soils over infertile, pre-Carboniferous rock types, such as Precambrian metamorphosed sediments and Ordovician conglomerate (Fig. 5D). Only at alpine altitudes, does it occur on other rock types such as Triassic sandstone or Jurassic doleritc.

Selected specimens examined (total = 58): AUSTRALIA, TASMANIA: Scotts Peak Road near airstrip, 43°02'S, 146°19'E, 340 m a.s.l., *G. Kantvilas & J. Jarman 86/91*, 13 Mar. 1991 (HO, distributed as *Lichenes Australasici Exsiccati No. 227*); Humboldt Divide, 42°43'S, 146°27'E, *G.*

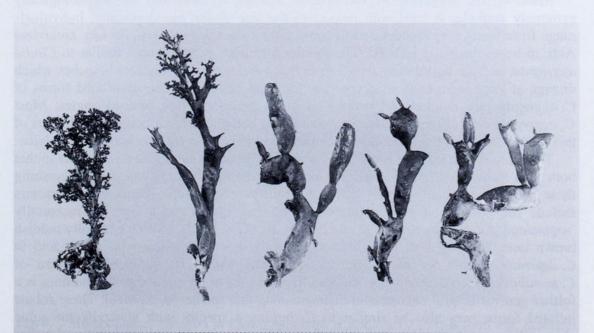


Fig. 8. Cladia moniliformis (Kantvilas 74/98); fertile pseudopodetia at left. Scale in mm.

Kantvilas s.n., 28 July 1986 (HO); Mt Norold, 43°15'S, 146°15'E, 950 m a.s.l., *G. Kantvilas 35/94*, 24 Feb. 1994 (HO); The Knob, 42°44'S, 145°58'E, 440 m a.s.l., *G. Kantvilas 189/95*, 5 Dec. 1995 (HO); 1.5 km SE of McPartlan Pass, 42°52'S, 146°12'E, 330 m a.s.l., *G. Kantvilas 194/95*, 5 Dec. 1995 (HO); Gordon River Road, 1 km E of Boyd Lookout, 42°49'S, 146°22'E, 560 m a.s.l., *G. Kantvilas 110/95*, 21 Sep. 1995 (HO).

6. Cladia mutabilis Kantvilas & Elix sp. nov.

Species *Cladiae inflatae* affinis sed habitu erecto, pseudopodetiis sterilibus apicibus acutis, pseudopodetiis fertilibus robustis excelsisque, sporis parvioribus, et modo acidum fumarprotocetraricum continenti praecipue divergens.

Type: Australia, Tasmania, The Knob, 42°44'S, 145°58'E, on soil at disturbed roadside edge in buttongrass moorland, 440 m a.s.l., 5 Dec. 1995, *G. Kantvilas 187/95* (holotype HO; isotype CANB).

Sterile pseudopodetia erect, forming clumps or spreading swards, slender, varying from evenly tapered and not inflated, to quite grossly inflated, dimpled and puckered, 20–60 mm tall, 0.4–5 mm wide, dichotomously or trichotomously branched up to 6 times, tapering to acute or sometimes awl-like apices containing pycnidia; surface smooth and mostly glossy, olive-brown to brown, olive-greenish in shade; axils closed, not constricted, forming angles of 20–45°; perforations abundant, 0.1–2 mm wide, ellipsoid or rather slit-like in very slender pseudopodetia, usually in rows to one side of the pseudopodetia; medullary cavity farinose, consistently whitish. *Fertile pseudopodetia* typically more robust and taller than the sterile pseudopodetia, usually discrete, often rather bulbously inflated to 7 mm at the base, then tapering to 2–4 mm wide, typically corymbose and highly perforate in the upper part. *Apothecia* apical, black, 0.1–0.25 mm wide when well-developed, proliferating with up to 6 tiers, clustered in groups of up to 9. Ascospores ellipsoid, 8–10 × 3–4.5 µm (rather rare). *Pycnidia* common, usually at the apices of sterile pseudopodetia. *Conidia* filiform, usually curved, (5–)6–8(-10) × 0.8–1.5 µm. (Fig. 9)

Chemistry: fumarprotocetraric acid; medulla K-, C-, KC-, Pd+ red, UV-.

Remarks: As suggested by the specific epithet, *C. mutabilis* is morphologically extremely variable, at least with respect to the size of the pseudopodetia. Individuals range from being very slender and filiform, rather like *Cladonia gracilis* ssp. *tenerrima* Ahti, to being distinctly inflated. The slender forms are perhaps most similar to *Cladia aggregata*, and are best distinguished from that species by their discrete branches which diverge at very acute angles. In contrast, the branches of slender, uninflated forms of *C. aggregata* are tangled and diverge at much broader (often obtuse) angles. Most *C. aggregata* also differ chemically in containing barbatic acid, although populations of this species which contain fumarprotocetraric acid may be sympatric with *C. mutabilis*.

The more robust inflated forms of *C. mutabilis* are most similar to *C. deformis* in that both taxa share a rather dimpled, puckered appearance. In such cases, distinguishing these species, especially sterile material, requires considerable care. Key characters include the constricted and at times perforate axils of *C. deformis*, its essentially 'segmented' form, even along a single branch, its blunt apices, and its generally reddish brown hue. The two taxa also differ chemically, but the presence of stictic acid in *C. deformis* should not be sought by spot tests alone. The branching pattern of *C. mutabilis*, which occasionally includes trichotomies or 'compressed' dichotomies is a further general helpful character in distinguishing this species in the field. These robust inflated forms may also be similar to *C. inflata*, a species with generally the same chemical composition. However, *C. inflata* differs by its decumbent habit and rather truncate pseudopodetia.

The distinctiveness of C. mutabilis is best seen in fertile material, which has the

Cladia aggregata complex

'typical' morphology of *C. aggregata* with markedly stouter fertile pseudopodetia carried above the sterile parts of the thallus. In *C. mutabilis*, these may be particularly robust and bulbous at the base, taper centrally and then expand in the upper part to the typical branched, perforate form. In contrast, in the other species of the complex, the fertile pseudopodetia are either of similar dimensions to the sterile ones (as in *C. inflata* and

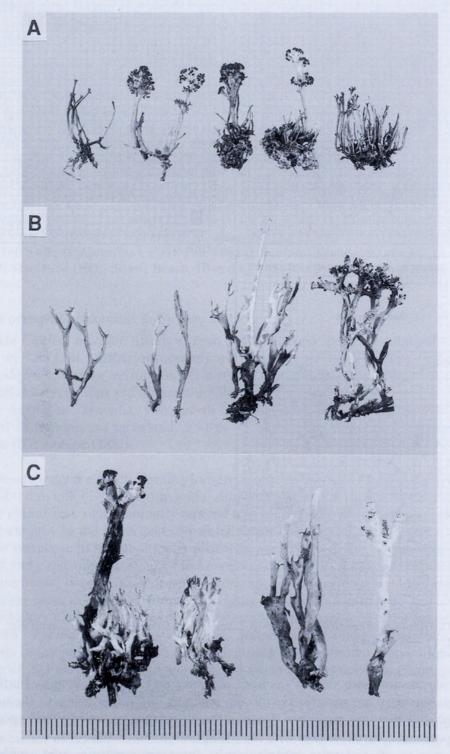


Fig. 9. Morphological variation in Cladia mutabilis. A Kantvilas 75/98; B from left: Kantvilas 197/95, Kantvilas s.n. (HO 114098), Kantvilas 75/98 (two clumps); C part of type (left) and Kantvilas s.n. (HO 114097) (right). Note the relatively robust fertile pseudopodetia. Scale in mm.

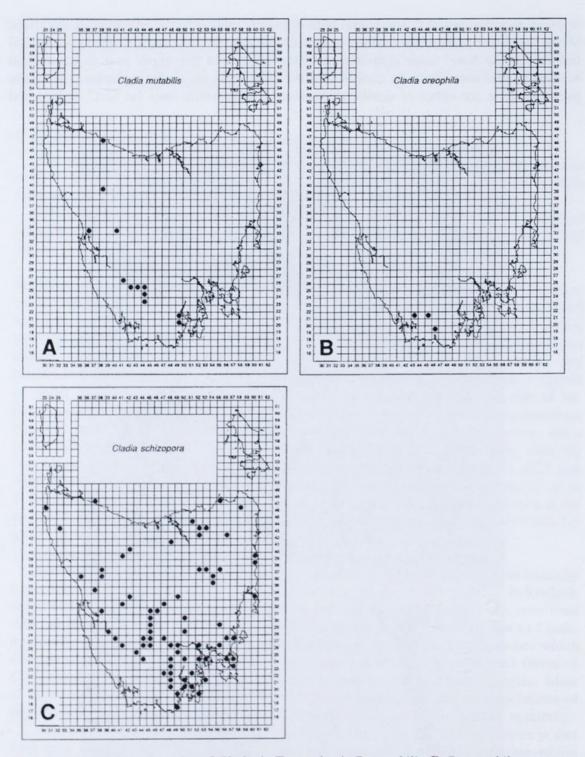


Fig. 10. Distribution of species of *Cladia* in Tasmania. A *C. mutabilis*; B *C. oreophila*; C *C. schizophora*.

C. dumicola) or are more slender (as in *C. deformis* and *C. moniliformis*). Furthermore, in *C. mutabilis* they are mostly corymbose, whereas in *C. aggregata*, *C. dumicola* and *C. moniliformis* they are racemose. Despite the abundance of well-formed apothecia in several specimens, very few asci with mature spores could be observed.

The species consistently contains only fumarprotocetraric acid, without any accompanying related substances. Only *C. oreophila* invariably shares this feature; *C. aggregata* often does, whereas *C. inflata* mostly contains additional related substances.

Distribution and ecology: Cladia mutabilis is endemic to Tasmania and, like most of its relatives, occurs mainly in the high rainfall peatlands of western Tasmania (Fig. 10A). It appears to be a lowland species (all collections are from below 650 m altitude), and also favours more sheltered, better drained conditions than do, for example, *C. moniliformis* or *C. deformis*. Thus the best developed thalli are found on rather deep, fibrous peaty soil at the scrubby edges of buttongrass moorland, on peat banks along road edges, and even in forest vegetation. It typically grows in association with *Cladonia southlandica*, *Siphula decumbens* and other species of *Cladia*, such as *C. inflata*, *C. retipora*, *C. sullivanii* and *C. aggregata*.

Specimens examined: AUSTRALIA, TASMANIA: Hermit Valley, 42°51'S, 146°08'E, 320 m a.s.l., *G. Kantvilas 193/95*, 5 Dec. 1995 (HO); same locality, 360 m a.s.l., *G. Kantvilas 180/80*, 17 May 1980 (HO); Queenstown-Strahan highway, 42°09'S, 145°25'E, 270 m a.s.l., *G. Kantvilas* s.n., 25 May 1986 (HO); Redan Hill, 42°08'S, 145°53'E, *G. Kantvilas* s.n., 27 Sep. 1986 (HO); foot of Sentinel Range, 42°52'S, 146°13'E, 360 m a.s.l., *G. Kantvilas 197/95*, 5 Dec. 1995 (HO); The Knob, 42°44'S, 145°58'E, 440 m a.s.l., *G. Kantvilas 190/95*, 5 Dec. 1995 (HO); Scotts Peak Road, *c.* 2 km N of Celtic Hill, 42°55'S, 146°22'E, 280 m a.s.l., *G. Kantvilas 98/95*, 21 Sep. 1995 (HO); Scotts Peak Road near the airstrip, 43°02'S, 146°19'E, 340 m a.s.l., *G. Kantvilas 96/95*, 21 Sep. 1995 (HO); Frodshams Pass, 42°49'S, 146°55'E, *G. C. Bratt & J.A. Cashin 2252*, 15 May 1965 (HO); south of Que River, 41°45'S, 145°50'E, 650 m a.s.l., *G. Kantvilas* s.n., 22 May 1986 (HO); Raminea Plains, 43°18'S, 146°54'E, *G. Kantvilas* s.n., 18 Feb. 1986 (HO); same locality, 80 m a.s.l., *G. Kantvilas 584/84*, 30 Mar. 1984 (HO); Sisters Beach, 10 m a.s.l., *J.A. Elix 23810*, 11 Jan. 1990 (CANB).

7. Cladia oreophila Kantvilas & Elix sp. nov.

Species *Cladiae mutabili* affinis et item pseudopodetia sparsim acutangulata ramosa habens et acidum fumarprotocetraricum continens, sed differt essentialiter pseudopodetiis scabridis, verrucosis vel areolatis, foraminibus absentibus vel rarissimis et apicibus decrescentibus sed aliquantum obtusis.

Type: Australia, Tasmania, 4 km north of Precipitous Bluff, 43°25'S, 146°36'E, on peaty soil in buttongrass moorland, 730 m a.s.l., 14 Feb. 1990, *G. Kantvilas 104/90* (holotype HO; isotype GZU).

Sterile pseudopedetia \pm erect, forming loosely, tangled swards or clumps, decaying at the base, 35–60 mm tall, (1–)1.5–5 mm wide, simple or sparsely \pm dichotomously branched, unevenly cylindrical, rather abruptly tapered to a blunt point, never awl-shaped; surface mottled pale grey in the lower part, brownish towards the apices, blackened at the base, scabrid to verrucose to bullate, usually distinctly areolate, with the areoles contiguous or dispersed and exposing a brown or blackened medulla; axils acute, forming an angle of 20–40°, perforate, not constricted; perforations absent to very rare, rounded and 0.4–0.8 mm wide or, more commonly, forming irregular fissures to 5 mm long and c. 0.3 mm wide; medullary cavity whitish to blackened, smooth to farinose. *Fertile pseudopodetia* not known. *Pycnidia* sparse to abundant, immersed in blunt, lobule-like thalline projections to 0.4 mm long and 0.3 mm wide, black to dark brown, rather glossy, apical in groups of 2–4 or, more commonly, scattered along the length of the pseudopodetium. *Conidia* not found. (Fig. 11)

Chemistry: fumarprotocetraric acid; medulla K-, c-, Pd+ red, UV-, KC-.

Remarks: The rather inflated pseudopodetia with unconstricted, acute-angled axils, and the presence of fumarprotocetraric acid alone, ally this species most closely to *Cladia mutabilis*. Nevertheless, *C. oreophila* is a very distinctive lichen, easily recognised in the field. The scabrid to areolate surface of its pseudopodetia is unique: the areoles are irregular to \pm stellate, and may be flat and contiguous to coalescing, or rather convex to bullate and dispersed over a blackened, exposed medulla. In sharp contrast, all other



Fig. 11. Cladia oreophila (part of type). Scale in mm.

species of the *C. aggregata-C. inflata* complex have a continuous to rather glossy cortex, even when growing in very exposed, wind-abraded habitats.

The near absence of perforations in *C. oreophila*, apart from in the axils, is also distinctive, and hence the species may sometimes resemble some species of *Cladonia* which have a similarly areolate-scabrid cortex. Perforations are also absent or almost so in *C. inflata*, but this species has a decumbent habit and some perforations are usually present on the underside. The rather blunt apices of the pseudopodetia of *C. oreophila* are similarly diagnostic, given that most related species of *Cladia*, excluding the grossly inflated-constricted species, *C. deformis* and *C. moniliformis*, have acute or awl-shaped apices containing pycnidia. When seen in well-developed colonies in the field, *C. oreophila* gives the impression of brown, crowded, finger-like lobes, protruding through a mat of graminoid monocotyledons, a little like the Northern Hemisphere alpine lichen genus *Dactylina*.

Apothecia and ascospores have not been found in *C. oreophila*. Nor have conidia been observed, despite the abundance of seemingly well-developed pycnidia in at least one specimen, and the pycnidia sectioned contained at most only tightly coiled hyphae.

Distribution and ecology: Cladia oreophila is a rare species known at present from only three locations in the remote mountain ranges of south-western Tasmania (Fig. 10B). Unlike the other species of *Cladia*, which have a rather broad ecological and altitudinal range, this new species appears to be exclusively alpine, hence the specific epithet 'oreophila' meaning 'mountain loving'. It occurs in exposed alpine heathlands and moorlands, typically in relatively open patches of low sedgeland-heathland dominated by *Carpha curvata*, *Dracophyllum milliganii*, *Empodisma minus* and *Oreobolus oligocephalus*. Common lichens with which *C. oreophila* is associated include *Cladia moniliformis*, *C. inflata*, *C. retipora* and *Siphula decumbens*.

Specimens examined: AUSTRALIA, TASMANIA: Mt Norold, 43°15'S, 146°15'E, 950 m a.s.l., G. Kantvilas 29/94, 24 Feb. 1994 (HO); Eastern Arthur Range, c. 1 km south of East Portal, 43°14'S, 146°26'E, 930 m a.s.l., G. Kantvilas 102/91, 25 Mar. 1991 (HO).

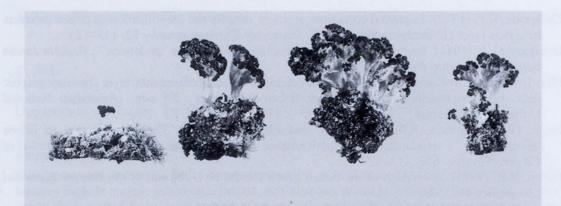


Fig. 12. Cladia schizopora (Kantvilas 8/98). Scale in mm.

8. *Cladia schizopora* (Nyl.) Nyl. in Hue, *Rev. Bot.* 6: 161 (1888). *Cladonia schizopora* Nyl., *Syn., Meth. Lich.*: 217 (1860). *Type*: Tasmania, supra truncos putridos, *C. Stuart* (holotype H-NYL, *n.v.*).

Cladia schizopora is the only sorediate species in the genus. It is further characterised by having very short, corymbose fertile pseudopodetia, mostly <15 mm tall but occasionally *c*. 20 mm tall in very moist, shaded habitats (Fig. 12). Soredia develop internally within the fertile pseudopodetia and at the apices of the sterile pseudopodetia, which may become reduced to a sorediate, subsquamulose mat. Some sterile specimens may be entirely sorediate and resemble a coarse *Lepraria*. This species contains fumar-protocetraric acid and traces of protocetraric acid; medulla Pd+ red, K-, KC-, C-, UV-. Further descriptions are provided by Galloway (1985) and Filson (1981, 1992).

Distribution and ecology: This species is known from southern Australia, New Zealand and southern Chile. In Tasmania it is widespread, mainly in lowland areas of low to medium rainfall, growing on bark, charcoal and lignum, or rarely on peaty soil (Fig. 10C). By far the most common host is *Eucalyptus*, where *C. schizopora* grows in association with *C. aggregata*, *Cladonia rigida* and *Neophyllis melacarpa*. In drier areas, additional associated lichens include *Thysanothecium scutellatum*, *Hypocenomyce australis* and *H. foveata*.

Selected specimens examined (total = 99): AUSTRALIA, TASMANIA: Moogara, 460 m a.s.l., *G. Kantvilas 30/80*, 10 Mar. 1980 (HO, BM); Anthony Road, 41°50'S, 145°38'E, *G. Kantvilas 241/91*, 10 May 1991 (HO); O'Grady's Gully, Mt Wellington, 42°55'S, 147°16'E, *A.V. Ratkowsky L81*, 16 Mar. 1981 (BM, HO); Franklin River Plains, 42°13'S, 146°02'E, 390 m a.s.l., *G.C. Bratt & M.H. Bratt*, 2 Jan. 1966 (HO); Comstock Mine, 41°55'S, 145°17'E, *G.C. Bratt 4040*, 30 Mar. 1969 (HO); Mueller Road, 42°49'S, 146°28'E, 550 m a.s.l., *G. Kantvilas 8/98*, 21 Feb, 1998 (HO).

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