

Standard Paper

Three new species of siphuloid lichens, with a first key to the genus *Parasiphula*

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Abstract

The term ‘siphuloid’ is introduced for a suite of distinct lichen genera with a superficially similar foliose to fruticose morphology, notably *Siphula*, *Siphulella*, *Siphulopsis*, *Parasiphula* and *Knightiellastrum*. Three new species are described: *Parasiphula squamosa* Kantvilas (from Tasmania and New Zealand), characterized by a whitish grey, squamulose or minutely foliose thallus lacking lichen substances or containing traces of atranorin; *Siphula capensis* Kantvilas (from southern Africa), containing baeomycesic and squamatic acids, and characterized by robust, broadly flattened, rounded lobes with thickened apices; and *S. crittendenii* (from the Caribbean but with an outlying collection from Queensland, Australia), an epiphytic species containing thamnolic acid, with fragile, flattened lobes mostly to 10 mm long and 1–5 mm wide, with ragged or much-divided apices. Salient features of the species of *Parasiphula* are summarized and a first key for this genus is presented. Infrageneric problems in *Siphula* are also discussed briefly.

Key words: Caribbean islands, *Coccotremataceae*, *Icmadophilaceae*, new species, southern Africa, Tasmania, taxonomy

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Introduction

Siphula Nyl. is a genus of foliose to fruticose lichens that had long bewildered taxonomists owing to its lack of ascumata and highly variable morphology and chemistry. Advances in the knowledge of the group over the last 50 years have seen the clarification and description of new species, mainly from New Zealand and Tasmania (Galloway 1983; Kantvilas 1987, 1994, 1996, 1998), mainland Australia (Kantvilas 2004), South-East Asia (Obermayer & Kantvilas 2003; Kantvilas *et al.* 2005), southern Africa (Mathey 1971; Kantvilas *et al.* 2003) and South America (Kantvilas & Elix 2002; Marcano 2021a, b). The first investigations of the phylogenetic position of *Siphula* (Platt & Spatafora 2000; Stenroos *et al.* 2002) placed it in the *Icmadophilaceae*. A subsequent molecular investigation by Grube & Kantvilas (2006), focusing on infrageneric groupings within *Siphula* inferred from morphology, secondary chemistry, ecology and distribution (Kantvilas 2002), found that the genus as traditionally understood could be divided into two, unrelated but highly morphologically convergent genera, and described the genus *Parasiphula* Kantvilas & Grube (*Coccotremataceae*). Earlier, another unusual lichen with a *Siphula*-like morphology, chemistry and ecology was described as the monotypic genus *Siphulella* Kantvilas *et al.* following the discovery of ascumata (Kantvilas *et al.* 1992). A further molecular study by Ludwig *et al.* (2020) again confirmed the phylogenetic position of *Siphula* and described two additional, morphologically

similar, monotypic genera, *Siphulopsis* Kantvilas & A. R. Nilsen and *Knightiellastrum* L. Ludw. & Kantvilas. Distinct though these genera are, especially to the field lichenologist, all share a superficially similar growth form, anatomy and ecology, as well as (apart from *Siphulella*) an absence of fruiting bodies. Here the term ‘siphuloid’ is coined for them, in much the same way as other morphological groups of often-unrelated lichens have been referred to as ‘cladoniiform’ (Stenroos & DePriest 1998), ‘baeomycetoid’ (Platt & Spatafora 1999) or ‘lecideoid’ (Hertel 1984). Whereas *Siphula* itself is \pm cosmopolitan, the other siphuloid genera display a distinctly austral cool temperate distribution, apart from *Siphulopsis* which is found in warm temperate Queensland, Australia.

The present paper continues the author’s long interest in siphuloid lichens, which has been fuelled by the predominance of these taxa in the wild, natural areas of Tasmania. In the course of delimiting the Tasmanian taxa, collections from many other parts of the world have been studied, revealing additional overlooked species. Here, a new Tasmanian species of *Parasiphula* is described, as well as two species of *Siphula* from the tropics and southern Africa. In addition, a first key to the species of *Parasiphula* is presented.

Materials and Methods

The study is based on specimens deposited in a range of herbaria as cited in the text, but principally from the Finnish Museum of Natural History (H), Michigan State University, Lansing (MSC), the Natural History Museum, London (BM), and the Tasmanian Herbarium (HO). Morphological examinations were undertaken at low power magnification; anatomy was studied at high power using thin, hand-cut sections of the thallus mounted in water, 10% KOH (K) and lactophenol cotton blue. The author has studied

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the new species in the field in Tasmania and on Puerto Rico during the excursions of the IMC in 2018. Chemical analyses are mandatory in identifying and delimiting siphuloid lichens and were undertaken routinely by thin-layer chromatography following standard methods (Orange *et al.* 2010); solvent A was the preferred medium. Standard spot tests, especially with K, are also useful but subtle differences in colour intensity must be treated with caution because the concentration of substances can vary, even across a single thallus.

Taxonomy

Parasiphula Kantvilas & Grube (Coccotremataceae)

The genus *Parasiphula* was introduced by Grube & Kantvilas (2006) to accommodate what Kantvilas (2002) had termed the *Siphula fragilis* and *S. complanata* groups on the basis of correlations in morphology and chemistry. The genus was strongly supported by DNA-sequence data (ITS and LSU), with its closest relationships being in the mainly crustose lichen family Coccotremataceae. It is characterized by a foliose to fruticose, or rarely \pm squamulose thallus, anchored to the substratum by basal tufts of terete, highly branched, root-like, pale brown rhizines, a green, unicellular photobiont with globose cells 5–12 μ m diam., and terete or flattened, isobilateral, corticate lobes that are usually a shade of pale yellowish grey, yellowish brown, dull grey or red-brown. Ascomata and conidiomata are unknown. Chemical composition consists of dibenzofuranes or depsidones, with several species lacking lichen substances.

Parasiphula consists of eight species restricted to cool to cold temperate regions of the Southern Hemisphere, with Tasmania being an undisputed centre of diversity as currently understood. It grows on peaty soil, mostly in treeless, windswept, wet environments, often submerged in shallow pools or at the fringes of small lakes. *Parasiphula* displays remarkable morphological similarities with *Siphula*, with the two genera having a similar habitat ecology, similar root-like rhizines, and lacking fruiting bodies, but, as shown by Grube & Kantvilas (2006), they are only distantly related, with *Siphula* classified in the Icmadophilaceae together with, for example, *Dibaeis* Clem., *Knightiella* Müll. Arg., *Siphulella* Kantvilas *et al.* and *Thamnotia* Ach. ex Schaer. These differences are further illustrated by the two genera supporting entirely different complements of parasitic fungi (Motiejūnaitė *et al.* 2019). Those on *Parasiphula* include the monotypic genus *Amylogalla* Suija *et al.*

With experience, the species of *Parasiphula* can be identified in the field, especially when growing in their typical habitat. However, when growing in non-optimum habitats, they can display very variable and convergent morphologies, making chemical analyses using TLC mandatory. Thallus colour can be a helpful character but this changes over time, and most species and specimens acquire a distinct pinkish tinge with storage. Table 1 summarizes many of their salient features and supplements the identification key (see below).

Parasiphula squamosa Kantvilas sp. nov.

Mycobank No.: MB 846941

Characterized by the unique combination of a whitish grey, squamulose or minutely foliose thallus and a chemical composition that sometimes includes traces of atranorin and chloroatranorin.

Type: Australia, Tasmania, Ben Lomond, Stonjeks Lookout, summit of Hamilton Crag, 41°32'S, 147°40'E, 1535 m elev., on skeletal soil over alpine dolerite boulders, 20 November 2021, G. Kantvilas 552/21 (HO—holotype).

(Fig. 1)

Thallus squamulose to small foliose, forming sparse to dense cushions to 6 mm thick, in section delimited by a cortex 10–20 μ m thick composed of isodiametric cells 5–13 μ m wide. *Photobiont* a unicellular green alga with globose cells 5–9 μ m diam., loosely to densely packed throughout the entire medulla. *Squamules* very brittle and fragile, plane, undulate or concave, broadening from a narrow base and sparingly branched in several planes, densely congested, erect, ascending or decumbent, 1.5–5 mm tall, 1–3(–4) mm wide at the widest point, 0.13–0.25 (–0.3) mm thick; surface dull grey or whitish grey, sometimes discoloured darkish grey due to an overlying weft of unidentified fungal hyphae, dimpled and puckered but not scabrid; apices rounded, unthickened, sometimes \pm crenulate, commonly cracked off, sometimes nodulose or with the ultimate segments \pm terete, erect or ascending, up to c. 0.25 mm wide, occasionally with terete lobes dominating the thallus and obscuring the flattened basal parts. *Rhizines* firmly buried within the substratum, pale greyish brown to grey, terete, branched, c. 0.15–0.5 mm thick at point of attachment to the lobes.

Ascomata and *conidiomata* unknown.

Chemistry. Nil or with traces of atranorin and chloroatranorin; cortex and medulla K \pm very pale yellowish, KC–, C–, P–, UV–.

Etymology. The specific epithet alludes to the growth form of the new species.

Distribution and ecology. The new species is known from Tasmania and New Zealand, but has only been studied *in situ* in the former region. Although widely distributed across Tasmania, and found on several different rock types including Precambrian quartzite, Ordovician conglomerate and Jurassic dolerite, most collections are from the north-eastern highlands. There it grows on exposed alpine dolerite boulders and rock plates in a low heathland-herbfield mosaic, or in the extensive lithoserres that predominate at high elevations. Unlike the other species of the genus, which mostly grow on a relatively well-developed soil, the new species occurs almost directly upon rock, with just the thinnest layer of soil accumulated around its rhizines. It is frequently intermixed with or overgrows the alpine moss *Andreaea*. The rock habitat is richly colonized by a wide variety of lichens, with the larger, more common species being *Cladia aggregata* (Sw.) Nyl., *Micarea oreina* Kantvilas & Coppins, *Parasiphula fragilis* (Hook. f. & Taylor) Kantvilas & Grube, *Stereocaulon caespitosum* Redinger, *Usnea torulosa* (Müll. Arg.) Zahlbr. and species of *Umbilicaria* Hoffm.

Remarks. *Parasiphula squamosa* is an enigmatic species that has taken many years of observation and study to resolve. In its typical provenance in the north-eastern Tasmanian highlands, it is relatively easily recognized by its characteristic whitish grey, squamulose or minutely foliose thallus, in combination with a chemical composition that sometimes includes traces of atranorin and chloroatranorin. However, these compounds usually occur at such low concentrations that they are easily missed by TLC and their

Table 1. Salient features of the species of *Parasiphula*. Distribution: Tas = Tasmania, Vic = Victoria (Australia); NZ = New Zealand.

	<i>P. comata</i>	<i>P. complanata</i>	<i>P. elixii</i>	<i>P. foliacea</i>	<i>P. fragilis</i>	<i>P. georginae</i>	<i>P. jamesii</i>	<i>P. squamosa</i>
Thallus	fruticose	fruticose	foliose to fruticose	foliose	foliose	fruticose	fruticose	squamulose to small foliose
Colour when dry	pale yellowish brown to brownish grey, later developing a pinkish tinge	pale yellowish grey to yellowish brown or dull grey, often with a pinkish tinge	pinkish grey, with pale to deep reddish brown apices	whitish grey, sometimes developing a faint pinkish or yellowish brown tinge	deep reddish brown	dull pale grey with a pinkish or yellowish brown tinge	ivory white	dull grey or whitish grey
Lobes	terete, densely branched and entangled	typically broadly flattened and strap-shaped, simple to sparsely branched	broadly flattened, sparsely branched, brittle and fragile	broadly flattened, sparsely branched, brittle and fragile	broadly flattened, sparsely branched, very brittle and fragile	broadly flattened to elongate and subterete, simple to sparsely branched	terete to subterete, simple or very sparingly branched	plane, undulate or concave, sparsely branched
Surface	mostly undulate and puckered	smooth to dimpled or puckered	minutely scabrid and areolate	markedly scabrid, areolate to verruculose	smooth throughout or occasionally slightly puckered	smooth to scabrid	smooth or undulate	dimpled and puckered
Lobe height	to 25 mm	to 50 mm	10(–25) mm	5–15 mm	2–10 mm	10–30 mm	(6–)12–35 mm	1.5–5 mm
Lobe width	0.2–0.5(–0.7) mm	0.5–5 mm	1–8 mm	4–12 mm	1–10 mm	3–5 mm	0.2–0.8 mm	1–3(–4) mm
Lobe thickness	-	0.12–0.25 mm	0.1–0.15 mm	0.1–0.15 mm	0.1–0.15 mm	0.15–0.25 mm	-	0.13–0.25(–0.3)
Chemistry	nil	porphyritic acid and methyl porphyrylate	lobaric acid	nil	nil	porphyritic acid	nil	atranorin (±)
Ecology	submerged in alpine environments	boggy alpine soil, often seasonally inundated	peaty or gravelly soil over rocks in heathland and/or montane habitats	peat-filled crevices on alpine boulders	wet peaty soil at high elevations, often inundated	peaty soil in rock crevices	wet soil in moorland	rocks, usually at alpine elevations
Distribution	Tas, South America	Tas, NZ, South America	Tas, NZ	Tas, NZ	Tas, Vic, NZ	Tas, NZ	Tas	Tas, NZ

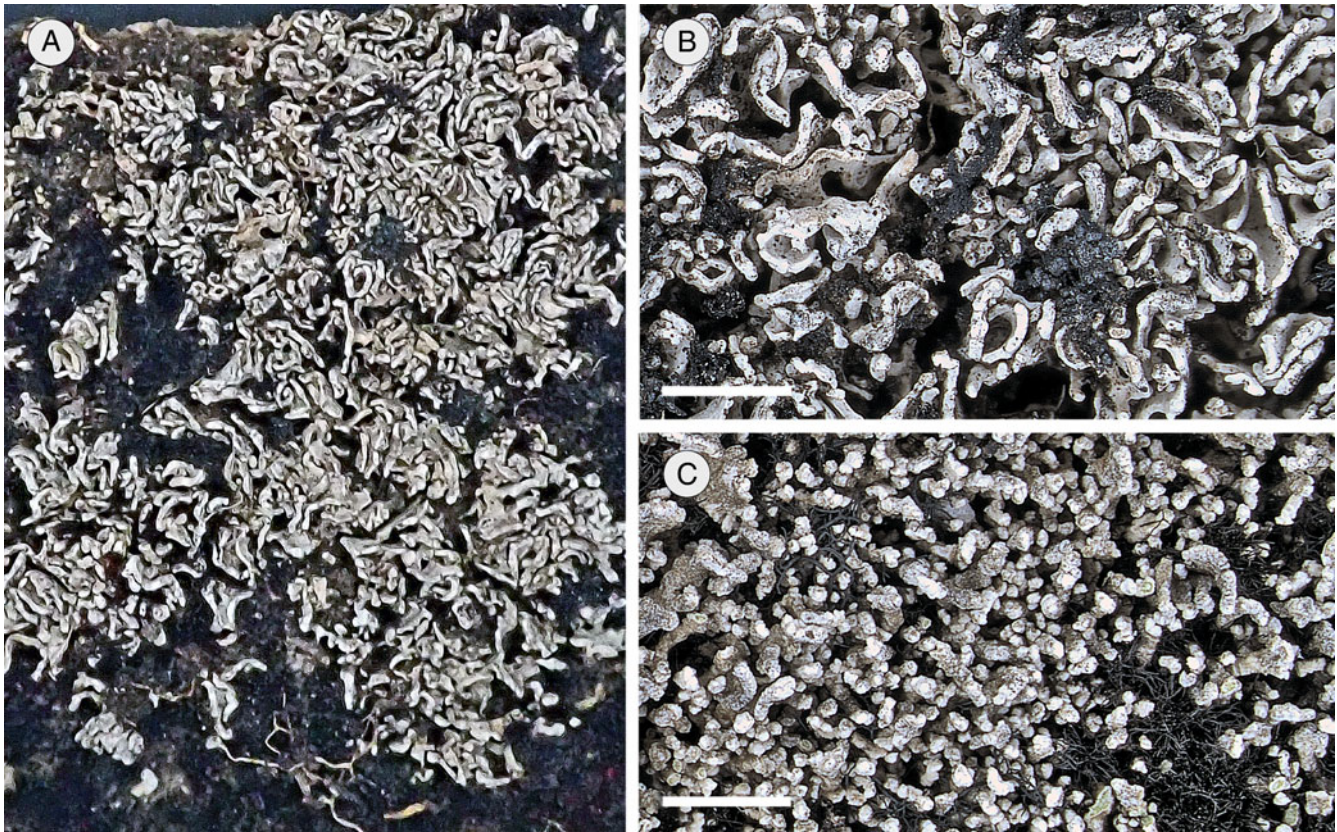


Fig. 1. *Parasiphula squamosa* habit. A, typical form with flattened, squamulose lobes (Kantvilas 12/97A). B, squamulose thallus detail (Kantvilas 12/97A). C, form with the ultimate segments of the squamules becoming terete (Kantvilas135/18). Scales = 2 mm. Images: Jean Jarman. In colour online.

presence was confirmed by HPLC (by Prof. J. Elix, Canberra). Away from its typical habitat, and in the wetter, western parts of Tasmania or at lower elevations, *P. squamosa* becomes more variable and easily confused with other species of the genus. The most similar is *P. georginae* (Kantvilas) Kantvilas & Grube, which differs unequivocally by containing porphyritic acid. In general, this species has a larger, more robust, fruticose thallus of flattened, ±erect lobes that form a dense mat in peat-filled rock crevices. However, in more exposed situations on thinner soil, its thallus can become highly reduced, with many subterete or nodulose lobes or lobe apices. Since *P. squamosa* and *P. georginae* can occur at the same sites and in the same habitats (although they have never been observed growing together), chemical analysis by TLC is mandatory to confirm their identification. The C+ slow greenish reaction of *P. georginae* cannot be relied upon. Superficially, the new species may also resemble the widespread *Siphula decumbens* Nyl., which can occur in similar habitats on alpine rocks, but that species is readily distinguished by its chalky white, scabrid thallus containing thamnolic acid (K+ yellow). Two species of *Parasiphula* that lack lichen substances are *P. jamesii* (Kantvilas) Kantvilas & Grube and *P. comata* (Nyl.) Kantvilas & Grube, but both have a thallus composed almost entirely of terete lobes. While terete lobes may be seen in *P. squamosa*, they tend to be the ultimate segments of branched, flattened lobes. Furthermore, the habitat of these species is completely different, with *P. comata* being sub-aquatic and *P. jamesii* occurring exclusively on wet, peaty or gravelly soil and never on exposed rocks. A further greyish white

species of *Parasiphula* that lacks lichen compounds is *P. foliacea* (D. J. Galloway) Kantvilas & Grube, but its lobes are broad and clearly foliose (up to 15 mm tall and to 12 mm wide), markedly scabrid, areolate to verruculose, and densely crowded together in mats; it is unlikely to be confused with *P. squamosa*.

Selected additional specimens examined. **Australia:** *Tasmania:* Mt Victoria, 41°19'S, 147°50'E, 1160 m, 1971, G. C. Bratt 71/58 et al. (HO); Mt Sprent summit, 42°48'S, 145°58'E, 1050 m, 1987, G. Kantvilas 44/87 (HO); summit of Mt Victoria, 41°20'S, 147°50'E, 1200 m, 1997, G. Kantvilas 12/97A (HO); St Patricks Head, 41°34'S, 148°14'E, 640 m, 1997, G. Kantvilas 122/97 (HO); summit of Schnells Ridge, 43°01'S, 146°26'E, 1085 m, 1998, G. Kantvilas 39/98 (HO); western flanks of Legges Tor, 43°32'S, 147°39'E, 1530 m, 1998, G. Kantvilas 112/98 (HO); Meadstone Falls, 41°45'S, 148°05'E, 400 m, 1999, G. Kantvilas 323/99 (HO); Maria Island, track to Mt Maria, 42°37'S, 148°06'E, 650 m, 2000, G. Kantvilas 204/00 (HO); Mt Sprent track, 42°47'S, 145°58'E, 900 m, 2003, G. Kantvilas 58/03 (GZU, HO); Clear Hill, 42°41'S, 146°16'E, 1030 m, 2021, G. Kantvilas 58/21 (HO); Ben Lomond, Plains of Heaven, 41°32'S, 147°39'E, 1500 m, 2021, G. Kantvilas 488/21 (HO); Legges Tor, 41°32'S, 147°39'E, 1560 m, 2022, G. Kantvilas 99/22 (HO); Ben Lomond, c. 750 m SE of Giblin Peak, 1530 m, 2022, G. Kantvilas 271/22 (HO); Ossians Throne, 41°33'S, 147°42'E, 1400 m, 2022, G. Kantvilas 345/22 (HO).—**New Zealand:** *South Island:* Denniston Plateau, c. 200 m from Whareatea escarpment mine, 1985, J. Johnston 1923 (HO).

Key to the species of *Parasiphula*

- 1 Lobes predominantly terete, at most flattened slightly only at the base; lichen substances always absent 2
 Lobes flattened, at most with some terminal segments terete to subterete; lichen substances sometimes present 3
- 2(1) Lobes simple, mostly erect, forming dispersed swards on moist soil **P. jamesii**
 Lobes densely branched and entangled, forming decumbent cushions or tufts, usually fully submerged in water **P. comata**
- 3(1) Thallus squamulose, lacking lichen substances or at most with traces of atranorin; growing on very thin soil, ±directly on rock **P. squamosa**
 Thallus foliose or fruticose, lacking lichen substances or containing porphyritic or lobaric acids; thallus typically growing on peaty or gravelly soil 4
- 4(3) Thallus fruticose, containing porphyritic acid (C+ slowly greenish); lobes relatively robust (up to 0.25 mm thick) and elongate 5
 Thallus foliose to fruticose, containing lobaric acid or lacking lichen substances (C–); lobes very thin, brittle and fragile (up to 0.15 mm thick), generally broadly rounded 6
- 5(4) Thallus containing porphyritic acid and methyl porphyrylate; commonly forming extensive swards in very moist or inundated habitats **P. complanata**
 Thallus containing porphyritic acid only; mostly forming tufts in peat-filled rock crevices at high elevations **P. georginae**
- 6(4) Lobes whitish grey, markedly scabrid, areolate to verruculose; lichen substances absent **P. foliacea**
 Lobes ±entirely red-brown or at least distinctly red-brown to reddish pink at the apices, smooth or minutely scabrid; lobaric acid present or lichen substances absent 7
- 7(6) Lobes typically entirely red-brown; lichen substances absent **P. fragilis**
 Lobes grey to pinkish grey with red-brown tints towards the lobe apices; containing lobaric acid
 **P. elixii**

New species of *Siphula*

Salient features of the genus *Siphula* s. str. have been outlined previously (Kantvilas 1998, 2002; Marcano 2021a, b). Like *Parasiphula*, it is characterized by an ecorticate, foliose, fruticose or, rarely, squamulose thallus, anchored to the substratum by basal tufts of highly-branched, root-like rhizines, and a green photobiont with globose cells 5–10 µm diam. Critically, *Siphula* contains depsides and/or chromones. This chemical difference offers the most practical means of separating *Siphula* from the morphologically similar *Parasiphula*, although with experience, individual specimens are unlikely to be ascribed to the wrong genus. Furthermore, in regions where both genera occur, such as cool temperate Australasia and southern South America, the species of *Siphula* invariably have a chalky white, scabrid thallus containing depsides (usually thamnolic, baeomycesic, squamatic or hypothamnolic acids).

Despite advances in the knowledge of the group, infrageneric problems within the core of *Siphula* remain. Ludwig *et al.* (2016, 2020) argued that *Siphula* could be further subdivided, with the depside-containing taxa placed in a distinct genus, leaving mainly the chromone-containing, Northern Hemisphere species, *S. ceratites* (Wahlenb.) Fr., in *Siphula*. Whilst there is some molecular support for this (e.g. see Grube & Kantvilas 2006; Ludwig *et al.* 2016, 2020), the status of several neotropical taxa, notably *S. pteruloides* Nyl. and *S. carassana* Müll. Arg., where depsides and chromones co-occur, requires investigation. There is also the distinct likelihood that sequences of two depside-containing taxa, *S. polyschides* Kremp. and *S. pickeringii* Tuck. (considered synonyms by Kantvilas (2002)) that cluster with *S. ceratites*, generated by Platt & Spatafora (2000) and reused by subsequent workers, are based on misidentifications, possibly of the chromone-containing neotropical species *S. pteruloides*.

Ascomata in *Siphula decumbens* and *S. fastigiata* (Nyl.) Nyl. were thought to have been detected by Ludwig *et al.* (2016), but subsequent examination of this material (this study) indicates that it represents the ascomata of the lichenicolous fungus *Aabaarnia siphulicola* Diederich. *Siphula* in general supports a rich suite of parasitic fungi across its geographical range, including the monotypic genera *Aabaarnia* Diederich and *Saania* Zhurb. (Motiejūnaitė *et al.* 2019).

New species of *Siphula* continue to be discovered, as demonstrated most recently by Marcano (2021a, b) who described four new species from the Venezuelan high páramo and the highlands of Guyana. Several further unidentified taxa remain in herbarium collections, chiefly from tropical South America and the Caribbean, suggesting that the study of *Siphula* will remain rewarding into the future. Two new species are described here.

Siphula capensis Kantvilas sp. nov.

Mycobank No.: MB 846942

Containing baeomycesic and squamatic acids, and distinguished from *S. fastigiata* and other chemically identical species by its robust, broadly flattened, smooth lobes, up to 8 mm wide and to 15 mm tall, with rounded, revolute or somewhat thickened apices.

Type: South Africa, Apollo Peak, Kromrivier, Cedarberg, S slope of ridge, E of peak, on shallow soil over bedrock, c. 1600 m elevation, 15 September 1984, H. C. Taylor 11054 (BM—holotype).

Siphula involuta R. Sant. nom. nud.

(Figs 2 & 3)



Fig. 2. *Siphula capensis* habit. Note the thickened apices (holotype). Scale = 2 mm. Image: J. Jarman. In colour online.

Thallus foliose when well developed, more rarely squamulose, forming a tight cushion or mat to c. 80 mm wide and up to 20 mm thick, in section delimited by a cortex 25–50 μm thick composed of densely packed, short hyphae 1.5–2.5 μm thick. *Photobiont* a unicellular green alga with globose cells 5–10 μm diam., occurring as an interrupted layer 50–65 μm thick or, more commonly, dispersed throughout the entire medulla. *Lobes* rather robust, plane, convoluted, sparingly branched, densely congested, erect or ascending, 2.5–8 mm wide, up to c. 5–15 mm tall, 0.3–0.5 mm thick; surface pale greyish or whitish, sometimes with a faint pale bluish hue, smooth or somewhat dimpled and puckered, sometimes a little scabrid; apices entire, typically a little revolute and therefore appearing rounded and somewhat thickened. *Rhizines* firmly buried within the substratum, pale beige to grey, terete, branched, c. 0.5–1 mm thick at point of attachment to the lobes.

Ascomata and *conidiomata* unknown.

Chemistry. Baeomycesic and squamatic acids; cortex and medulla $\text{K}\pm$ pale yellowish, $\text{KC}-$, $\text{C}-$, $\text{P}+$ pale orange-yellow, $\text{UV}+$ yellow.

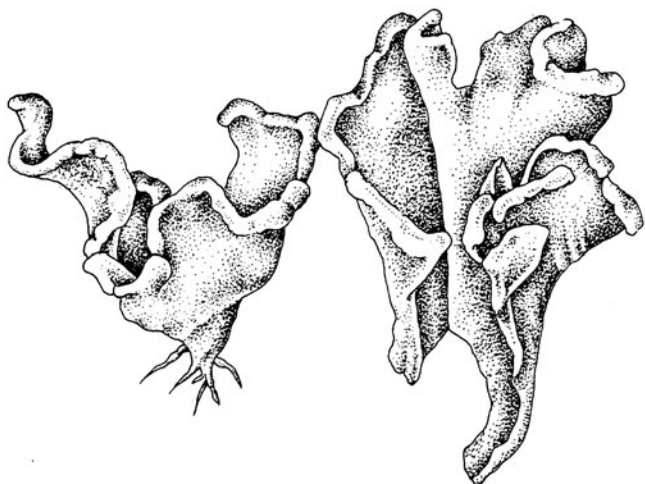


Fig. 3. *Siphula capensis* habit (holotype). Drawing: Lauren Black.

Etymology. The specific epithet refers to the provenance of the new taxon at the Cape of Good Hope, South Africa.

Distribution and ecology. I have not observed this taxon in the field and label data offers scant ecological information other than that the species occurs on soil. All collections are from the Cape.

Remarks. The baeomycesic and squamatic acid chemosyndrome is common and geographically very widely distributed in the genus *Siphula*. The new species is distinguished from these chiefly by its robust, relatively broad (as distinct from elongate) lobes with very distinctively thickened, seemingly rolled apices (Figs 2 & 3). This feature earned the new taxon the herbarium name of '*S. involuta*', which has been pencilled onto several herbarium specimens (e.g. in H and BM) by the late Rolf Santesson, a specialist of the group. Whilst I would have preferred to validate Santesson's name here, I have opted not to because this invalid, unpublished name has found its way into *de facto* use through herbarium databases (e.g. MycoBank, Consortium of North American lichens), and to validate it now with a different authority could well cause confusion.

Mathey (1971) clearly encountered *S. capensis* in her study of African species, even illustrating it (op. cit.: figs 26–28), but she included it within her very broad (and untenable) concept of *S. decumbens*. That species contains thamnolic acid and, although highly variable, its variation never encompasses the distinctive morphology of *S. capensis*.

The thickened lobe margins of *S. capensis* are also seen in the Australian *S. coriacea* Nyl., but that species contains barbatic acid and has more elongate lobes with a pale bluish grey hue. In the African region, the new species has no confusing species. *Siphula dissoluta* Nyl. (hypothamnolic acid), *S. decumbens* (thamnolic acid) and *S. fastigiata* (baeomycesic/squamatic acids) all differ clearly in having a very brittle, chalky white thallus with a markedly scabrid or mealy surface. The Cape endemic, *S. torulosa* (Thunb. ex Ach.) Nyl., is chemically identical but differs by its narrow, brittle lobes and entangled, decumbent habit. Some specimens of *S. capensis* are infected by the lichenicolous parasite *Saania mobergii* Zhurb.

Specimens examined. **South Africa:** *Western Cape:* Cap Bona Spei (H-NYL 40186, 40189); summit of Mt Tabularis (H-NYL 40189); *Fl. Cap.* 502 (BM); Worcester Distr., Deception Peak, Waachhoek plateau, 5000 ft [1500 m], 1942, *T. F. Stokes* s. n. (UPS); Clanwilliam Distr., Scorpionsberg, N Cedarberg, 5300 ft [1590 m], 1945, *E. Esterhuysen* 12279 (UPS); Cedarberg, c. 100 miles [160 km] N of Cape Town, c. 4500 ft [1350 m], 1985, *E. Abdy* 1 (BM); Piketberg, Grootberg Mtn, 32°47'S, 18°39'E, 800 m, 1996, *R. Moberg* 11758 (distributed as *Lich. Sel. Exsicc. Upsaliensis* 290 (CANB, H, UPS)).

***Siphula crittendenii* Kantvilas sp. nov.**

MycoBank No.: MB 846943

Characterized by a chalky white thallus containing thamnolic acid, with brittle, flattened lobes mostly up to 10 mm long and 1–5 mm wide, with the apices gnarled and granular, ragged and lacerate, or much-divided into narrowly flattened or subterete branchlets.

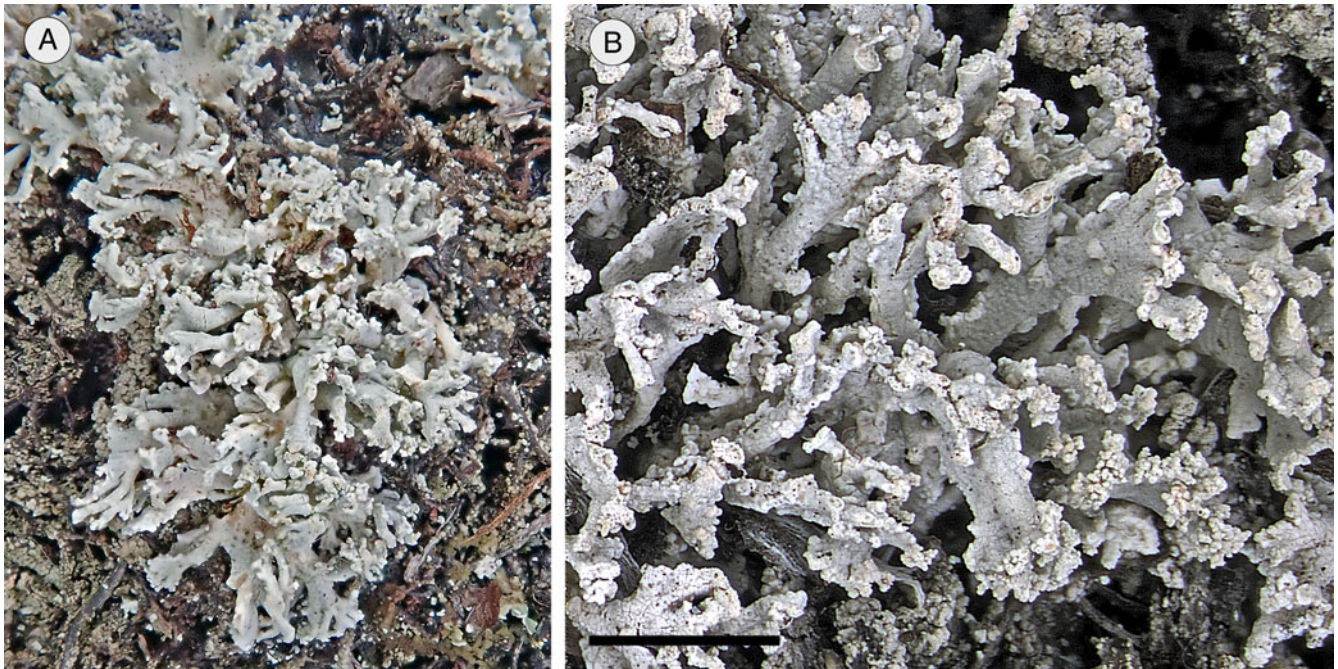


Fig. 4. *Siphula crittendenii* (holotype). A, general habit. B, detail showing the lacerate lobes with gnarled, granular apices. Scales = 2 mm. Images: Jean Jarman. In colour online.

Type: Puerto Rico, Carite State Forest, c. 14.5 km E of Cayey, 18°05'N, 66°02'W, on canopy branches of a fallen tree in forest, 18 July 2018, G. Kantvilas & P. Crittenden (HO—holotype; F—iso-type).

(Fig. 4)

Thallus small fruticose, typically forming discrete or contiguous tufts 5–10(–30) mm across and up to 10(–25) mm tall, more rarely comprising scattered, single, flabellate lobes; in section ecorticate or with a poorly differentiated layer of densely packed hyphae c. 20 µm thick. *Photobiont* a unicellular green alga with globose cells 4–8 µm diam., mostly concentrated in a band c. 20 µm wide towards the dorsal surface. *Lobes* brittle and fragile, plane, undulate or concave, sometimes twisted and involute, erect, ascending or decumbent, discrete or loosely entangled, occasionally with a somewhat thickened midrib, broadening from a narrow base and dividing unevenly in several planes, 4–10(–20) mm long, 1–5 mm wide at the widest point, 0.25–0.5 mm thick, towards the apices becoming much divided into narrowly flattened to subterete branchlets 0.2–0.5 mm wide, gnarled, granular and 0.15–0.2 mm wide at the tips, or occasionally with the apices ragged and lacerate; surface chalky white, dimpled and puckered, occasionally fenestrate, smooth or, more typically, scabrid, particularly on one side; margins entire or ragged, not thickened. *Rhizines* pale greyish brown to grey, terete, branched, c. 0.15–0.25 mm thick at point of attachment to the lobes.

Ascomata and *conidiomata* unknown.

Chemistry. Thamnolic acid; cortex and medulla K+ bright yellow, KC–, C–, P+ yellow-orange, UV–.

Etymology. Named in honour of Prof. Peter D. Crittenden (Nottingham, United Kingdom), co-collector of the type

specimen, a good friend and frequent companion on excursions to remarkable places.

Distribution and ecology. On the basis of herbarium collections, *S. crittendenii* is found mainly in the Caribbean Islands, where it occurs as an epiphyte on mossy trunks in low, scrubby forest. Henry Imshaug, collector of most material studied, frequently described the vegetation as ‘elfin forest’, ‘montane thicket’ and ‘mossy forest’ on his labels. The author’s observations on Puerto Rico suggest it grows in relatively well-lit situations on large canopy branches or trunks in forest gaps, forming tufts that protrude from epiphytic bryophytes. The single Australian specimen is ascribed to *S. crittendenii* with some caution, given the geographical disjunction between it and the Caribbean material. Clearly more Australian collections and observations are required but it is noteworthy that the habitat ecology of this collection, from the trunk of *Leptospermum wooroonooran* in low, scrubby, mixed microphyll-notophyll forest on a rocky knoll, is very similar to that of the Caribbean material.

Remarks. This taxon was first studied in the course of a revision of Tasmanian *Siphula* species (Kantvilas 1998), where it was included tentatively under *S. decumbens*, noting that further specimens may well reveal it to be distinct. The opportunity to observe this species in the field on Puerto Rico (during the IMC field trips in 2018) and to study the extensive collections of the late Henry Imshaug (held in MSC with some duplicates distributed elsewhere) have confirmed that it is indeed distinct from *S. decumbens*, albeit sharing the same chemistry.

Imshaug’s collections offer an excellent insight into the morphological variability of *S. crittendenii*. The typical form comprises a flattened, flabellate thallus that becomes much divided towards the apices into narrowly flattened to subterete, mostly ±erect branchlets. Critically, the lobe apices frequently become gnarled or granular. Such forms predominate in Imshaug’s

collections, all collected from scrubby vegetation at higher elevations on Caribbean Islands. When well developed, the thallus consists of much-branched tufts protruding from a mat of epiphytic bryophytes. The tufts are mostly up to 10 mm tall, but in one specimen (from Jamaica) they are as tall as 30 mm. When poorly developed, or perhaps, more accurately, immature, the thallus consists of single, scattered, flabellate lobes with ragged or torn apices but no branchlets. The range of specimens available allows these superficially different-looking forms to be interpreted as a continuum of development.

In contrast, *Siphula decumbens* is an extremely variable species when viewed across its broad range that includes Tasmania and New Zealand, the western Pacific and New Guinea, eastern Asia from Sri Lanka to Japan, southern Africa, the East African highlands and Mascarene Islands, and tropical America (but not the Caribbean). It is characterized by chalky white, usually broadly flattened scabrid lobes that form dense, decumbent mats or erect swards binding soil, or epiphytic tufts. Unlike *S. crittendenii*, its lobe apices are generally rounded and entire, sometimes thickened or crenulate, lobulate and nodulose but never subterete, gnarled or granular. To include under *S. decumbens* what is described here as *S. crittendenii* would mean broadening its morphological range to an untenable degree. An extreme epiphytic form with tufted, lacerate, fenestrate lobes seen in Tasmanian and New Zealand rainforests is rather similar to *S. crittendenii*, but these austral forms are seen as an *in situ* ecologically-driven continuum. In contrast, the morphology of *S. crittendenii* is essentially uniform.


The genus *Siphula* is well represented in the Neotropics, with several taxa containing thamnolic acid, including *S. carassana* (with additional siphulin), *S. chimantensis* V. Marcano (with additional hypothamnolic acid), the widespread *S. decumbens* and *S. pteruloides* (sometimes with additional siphulin). However, only *S. crittendenii* is known from the Caribbean Islands. An additional, as yet undetermined species is represented by three specimens from Dominica. These feature a rather reduced thallus of short, congested, gnarled lobes, growing on soil and are all from the same locality. Despite being morphologically very similar, one contains thamnolic acid only, another squamatic acid only and the third contains both squamatic and thamnolic acids (an unusual combination). Many more additional collections would be required to interpret these satisfactorily. I am loath to include them under *S. crittendenii* even provisionally, although typical *S. crittendenii* is also present on Dominica.

Selected specimens examined. **St Lucia:** Quarter of Soufrière: road south of Piton Canarie, 1963, 1800–2000 ft [540–600 m], *H. A. Imshaug* 29932, 29756 & *F. H. Imshaug* (CANB, MSC).—**Jamaica:** summit of Sugarloaf, 7100 ft [2130 m], 1953, *H. A. Imshaug* 15425, 15455 (MSC).—**Puerto Rico:** Humacao District: Luqillo Mountains, El Yunque, 700 m, 1967, *I. Landrón* 153, 255 (MSC); Luqillo Mountains, Palm Brake, La Mina, 550 m, 1967, *I. Landrón* 988 (MSC).—**Grenada:** summit of Mt Quaqua, 2250 ft [675 m], 1953, *H. A. Imshaug* 16111 (MSC); valley between Grand Etang and ridge from Mt Sinai to Mt Lebanon, 1400 ft [420 m], 1953, *H. A. Imshaug* 16120 (MSC); southern slope of Fedon's Camp, 2000–2100 ft [600–630 m], 1953, *H. A. Imshaug* 16215 (MSC).—**Guadeloupe:** Basse-Terre Island: summit plateau of La Soufrière, 1400–1484 m, 1963, *H. A. Imshaug* 33583, 33578 & *F. H. Imshaug* (MSC); Savana à Mulets, 1000–1100 m, 1963, *H. A. Imshaug* 33599 & *F. H. Imshaug* (MSC).—**Dominica:**

main ridge above Trois Pitons River (South Branch), 2900–3150 ft [870–940 m], 1963, *H. A. Imshaug* 33081 & *F. H. Imshaug* (H, MSC). *Parish of St George:* Laudat, Sandringham Estate, 1800–2200 ft [540–660 m], 1963, *H. A. Imshaug* 33080 & *F. H. Imshaug* (MSC).—**Dominican Republic:** Cordillera Central, ridge between Pico del Yaque and L. Chinguela, 6800 ft [2040 m], 1958, *H. A. Imshaug* & *C. M. Wetmore* 3752, 3744 (CANB, MSC).—**Trinidad and Tobago:** *Trinidad:* summit area of El Tucuche, 3000–3072 ft [900 m], 1963, *H. A. Imshaug* 31935, 31910 & *F. H. Imshaug* (MSC).—**Australia:** *Queensland:* Mt Lewis-Carbine Tableland, near Mt Lewis Hut, 16°30'47"S, 145°16'06"E, 1220 m, 2018, *G. Kantvilas* 435/18 (CNS, HO).

Specimens of unidentified species examined. **Dominica:** Valley of Desolation and Boiling Lake, 2500 ft [750 m], 1963, *H. A. Imshaug* 33103 (thamnolic and squamatic acids) (MSC); *ibid.*, *H. A. Imshaug* 33102 (thamnolic acid) (MSC); *ibid.*, *H. A. Imshaug* 33104 (squamatic acid) (MSC).

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