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# Authors' contributions

HBO: conceived, designed, and coordinated the study, examined herbarium specimens, completed the map and wrote the manuscript: VP: studied herbarium material, completed illustrations and wrote the manuscript; SLG: examined herbarium specimens and wrote the manuscript

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# **Competing interests**

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# **ORIGINAL RESEARCH PAPER**

# A brief survey of bryological studies in the Subantarctic, including Macrocoma tenue (Orthotrichaceae), a moss genus and species newly found in Îles Kerguelen

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# Abstract

Studies on the bryophyte flora of the Southern Ocean islands and in the Antarctic are briefly reviewed and the current state of knowledge of the moss flora of Îles Kerguelen is discussed. Macrocoma tenue (Hook. & Grev.) Vitt is recorded from the Îles Kerguelen archipelago and this constitutes the first record of the genus Macrocoma (Müll. Hal.) Grout from the Subantarctic. The local plants of the species are characterized and illustrated and their ecology is discussed. Global distribution of *M. tenue* is reviewed and mapped. It is suggested that the type subspecies of *M. tenue* is a Gondwanan relictual taxon, which could have evolved on this supercontinent prior to its break-up and, subsequently, it reached Îles Kerguelen where it survived during the Pleistocene glacial epoch.

# **Keywords**

Antarctica; austral polar regions; biodiversity; biogeography; Bryophyta; Kerguelen Biogeographical Province; Southern Ocean

# Introduction

The cool and cold areas in the Southern Hemisphere centered on the South Pole consist of the largely ice-covered Antarctic continent and a number of small and highly isolated islands or groups of islands widely scattered in the vast Southern Ocean. The delimitation and subdivision of the austral polar regions have been the subject of much discussion and controversy [1]. Subdivision of this region into at least two distinct biomes is now generally accepted. The southernmost part represents the Antarctic biome in its strict sense and consists of all lands and seas south of latitude 60°S, together with some peri-Antarctic islands. The South Sandwich Islands archipelago in the Scotia Arc and the orphaned Bouvetøya in the South Atlantic Ocean, both of which lie a little north of lat. 60°S, are also included to the Antarctic biome because of their similar climate and terrestrial vegetation [1]. The northern limit of the Antarctic biome is delimited by the Antarctic Convergence or Polar Frontal Zone, a seasonally varying oceanic boundary encircling Antarctica, where cold northward-flowing Antarctic waters meet and sink below the relatively warmer waters of the Subantarctic.

The second biome in austral polar regions is Subantarctica, situated at the northern periphery of the Antarctic biome and lying between the Antarctic and Subtropical Convergences. The latter separates the subantarctic waters of the West Wind Drift from the subtropical waters, which differ in their biological as well as chemical and physical

properties. The subantarctic islands are situated in a latitudinal belt around 50° to 55°S and all experience strong variation in daylight hours between summer and winter. Some, including South Georgia, Heard Island, and McDonald Islands, lie slightly to the south of the Antarctic Polar Frontal Zone, while the Prince Edward Islands, Îles Crozet, and Macquarie Island lie slightly to the north. The archipelago of Îles Kerguelen straddles the zone. All subantarctic islands are oceanic, located far from continental land masses, and their climate is strongly influenced by their location in the Southern Ocean, in close proximity to the Antarctic Polar Frontal Zone, ensuring that the climate of all the subantarctic islands is cool, wet, and windy. They lack arborescent vegetation but include tall tussock grasslands, megaherbs, short grasslands, mires, and tundra-like vegetation. The flora is dominated by bryophytes and lichens, whilst vascular plants predominate generally in the vegetation near sea level and at low altitudes. Additionally, upland fellfield may have significant cover of, for instance, *Azorella selago* Hook. f. and low grasses and sedges may also be relatively abundant.

Apart from the subantarctic islands, in the Southern Ocean there are a number of cool temperate oceanic island groups situated a little to the north. These include Auckland Islands, Campbell Islands, Antipodes Islands, Snares Island, and Bounty Island in the New Zealand region in the South Pacific Ocean; Tristan da Cunha, Nightingale Island, Inaccessible Island, and Gough Island in the middle of the South Atlantic Ocean; Falkland Islands in the west of the South Atlantic Ocean; and Île Amsterdam and Île Saint-Paul in the South Indian Ocean.

# Studies on the bryophyte flora of the Subantarctic

Antarctica is the only biome in the austral polar region, which is best known bryologically, and it is the only area in the Southern Hemisphere which received modern descriptive floras of hepatics and mosses. Its liverwort flora comprises 28 species [2–5], while the moss flora consists of 116 species and two varieties [6–8].

Although bryophytes are a dominant component of the vegetation, their flora on the subantarctic islands is still imperfectly known and the number of species either for the entire biome or most of the individual islands cannot be precisely given. At present, the only descriptive moss flora is that of Macquarie Island [9], although since its publication, several additional species have been recorded [10–13]. A synoptic moss flora of South Georgia, initiated by Greene [14], has never been completed although no fewer than 12 parts appeared, and with the publication of the genus *Vittia* Ochyra [15] the project ceased. However, the moss flora of this subantarctic island is well documented [16–22].

Checklists of liverworts and mosses are available for the Prince Edward Islands [23,24] and hepatics of South Georgia [25], Îles Kerguelen [26], Heard Island [27], Île Amsterdam [28], and the islands in the Kerguelen Biogeographical Province [29], as well as Macquarie Island [30] and Tristan da Cunha [31]. However, numerous liverwort and moss species have been added to the floras of the individual islands [11,32–49].

The moss flora of the islands in the Kerguelen Biogeographical Province in the South Indian Ocean is still inadequately studied, although they are phytogeographically the most interesting in the Subantarctic. These small specks of land are very isolated and logistically not easily accessible, but this province is a significant center of endemism with some 20 taxa [50–55] and one genus [56] of moss endemic to this region.

Among the four archipelagoes or island groups in this province, the Prince Edward Islands have the best studied moss flora, consisting of about 100 species [57–64]. Likewise, the highly isolated and heavily glaciated Heard Island has a fairly well studied moss flora [65,66] consisting of about 60 species. In contrast, the moss flora of Îles Crozet was least known until the late 1970s and about 40 species have so far been recorded from Île de la Possession and Île de l'Est, the two largest islands of this archipelago [67,68]. Subsequent field studies have added over 30 additional species to the moss flora [5,49,69–74] and the taxonomic status of some species described from Îles Crozet has been clarified [75–77].

The richest moss flora in this province is in the Îles Kerguelen archipelago, the largest land exposure in the Subantarctic with 7,215 km<sup>2</sup>. After South Georgia (120 Ma), it is, together with Heard Island, the second oldest subantarctic archipelago (40 Ma) in

the Subantarctic. It was explored during several expeditions in the nineteenth and in the first quarter of the twentieth century and moss collections were also made. They were studied mainly by European bryologists, resulting in about 115 new species being described with about the same number of previously described species also recorded [78–89]. Subsequent revisionary studies on these new taxa revealed the conspecificity of the great majority of them with species described earlier from other regions of the world [90–102]. The moss flora of Îles Kerguelen had about 125 species at the end of the twentieth century. However, this number has increased markedly in the last 2 decades when professional botanists and bryologists conducted field studies in this area, resulting in about 20 additional species of moss in Îles Kerguelen [72,103,104], including two as new to science [105,106]. In the present account, *Macrocoma tenue* (Hook. & Grev.) Vitt, is added to the moss flora of the Îles Crozet archipelago and represents the first report of the genus in the Subantarctic biome.

# Material and methods

The present study is based on the specimens which were collected on Îles Kerguelen in 2006–2007 during the bryological survey of the archipelago. They are currently housed in the bryophyte herbarium in the W. Szafer Institute of Botany of the Polish Academy of Sciences (KRAM). Mosses were identified by routine microscopic and laboratory techniques. Photographs of the habit and anatomical details were taken using an E-600 Olympus camera mounted on an Olympus SZ61 binocular microscope and Olympus BX53 microscope. The distribution map was generated using CorelDraw X7(64-bit) software.

# Results: subantarctic representation of Macrocoma

# An overview of the genus

Macrocoma (Hornsch. ex Müll. Hal.) Grout is a small genus of the Orthotrichaceae subf. Macromitrioideae that was split from the large genus Macromitrium Brid. [107], within which it was originally recognized as a separate section, Macromitrium sect. Macrocoma Hornsch. ex Müll. Hal. [108]. It is distinguished at a glance from other genera of the subfamily Macromitrioideae by the overall appearance of the plants which are slender and filiform and usually grow in loose or dense tangled mats. The primary stems are creeping, irregularly to subpinnately branched, with slender and widely spaced, erectascending branches which often have short secondary branchlets. The leaves are small, up to about 1.8 mm long, straight, nondecurrent, closely and stiffly erect-appressed to imbricate on drying, ligulate or ovate-lanceolate and narrowly obtuse, acute or acuminate at the apex, with entire or roughened margins that are plane throughout or recurved on one side below. The laminal cells are small, rounded to oval throughout the leaf or only elliptic and slightly elongate near the base, firm- to thick-walled, smooth to mammillose and plane to bulging but never papillose. Fertile plants are easily recognized by having very large, long conic-elliptic mitrate calyptrae which cover the entire capsules. Species of Macrocoma have often been merged with Macromitrium, but this genus differs in the presence of linear basal leaf cells. Macrocoma shares rounded basal leaf cells with Groutiella H. A. Crum & Steere but the leaves in this genus have a distinct pluriseriate basal marginal border of linear cells.

The genus *Macrocoma* has been well circumscribed by Vitt [109] who placed in it eight species. Later, the concept of the genus was expanded [110] and three additional species were included. They were divided into two subgenera, namely the type subgenus and *Macrocoma* subg. *Trachyphyllum* (Broth.) Vitt. The latter contained only two species which are narrow endemics of southern South America. Subsequently, this subgenus was segregated as the genus *Matteria* Goffinet [111]. Thus, the narrowly conceived genus *Macrocoma* consists of nine species (one with two subspecies) which are primarily distributed in the tropics of America, in tropical Africa and in tropical

and subtropical continental Southeast and East Asia, and only slightly penetrate into the subtropical and warm temperate zone in eastern North America and Asia. Additionally, species of *Macrocoma* occur at highly isolated stations in the Hawaiian Islands and the subtropical and warm temperate regions in eastern Australia and New Zealand [112]. Herein, the genus is recorded for the first time from the Subantarctic where it is represented by the type subspecies of *M. tenue* (Hook. & Grev.) Vitt, which was discovered in Îles Kerguelen.

#### Characterization of subantarctic plants of Macrocoma tenue

*Macrocoma tenue* was collected at a single locality in the southern part of Val Studer on Grande Terre, the largest island of the Îles Kerguelen archipelago during a bryological survey of this area in 2006–2007. Typically, *M. tenue* is an epiphyte growing on bark of tree boles and branches throughout its wide geographical range but occasionally it is found also growing epipetrically on rocks, for example in Africa [113], New Zealand (as *Macromitrium eucalyptorum* Hampe & Müll. Hal.) [114], and Japan (as *Macromitrium hymenostomum* Mont.) [115]. Because subantarctic islands lack arborescent vegetation, the species grows in Îles Kerguelen exclusively on rocks or on thin soil covering rocks, but such ecological vicariance is found in many typically epiphytic mosses throughout the world. The species occurs in exposed and sunny sites, usually in dry places, although some patches of the species growing not very high above the water level in the river are often splashed or sprinkled with water. It forms pure monospecific mats and only occasionally some shoots of *Catagonium nitens* (Brid.) Cardot and *Bucklandiella pachydictyon* (Cardot) Bedn.-Ochyra & Ochyra have been found as admixtures at the edges of mats. All plants of *M. tenue* from Îles Kerguelen lack sporophytes (Fig. 1).

Despite growing on atypical rupicolous sites and being sterile, the plants of Macrocoma *tenue* from Îles Kerguelen perfectly correspond with those from other parts of its wide geographical range and their identity is unequivocal. They are small, slender, and rigid plants, growing in dense, intricate mats, dull to somewhat glossy, brown to reddishbrown almost throughout except for the younger terminal portions of branches which are usually yellowish-green to yellowish-brown. The stems are creeping, 3 cm or more long, irregularly or more or less pinnately branched, with clusters of brown rhizoids along the side facing the substrate. The branches are numerous, erect-ascending or horizontal, 3-5 mm long, simple or branched. The axillary hairs are filiform, composed of three-seven short, brownish cells. The stem and branch leaves are similar in size and shape, the former being often somewhat reflexed and longer, to 0.9 mm (typically 0.7–0.8 mm long in branch leaves), 0.3–0.4 mm wide, erect-appressed when dry, erect-spreading to widely spreading when wet, straight or occasionally somewhat falcate, lanceolate to ovate-lanceolate or infrequently lanceolate-ligulate, often narrowly keeled above and broadly concave below. The leaf apex is bluntly acute or narrowly obtuse to broadly acuminate and often incurved. The margins are plane above, broadly recurved on one side below, entire or crenulate, especially in the proximal part because of strongly bulging mammillose cells. The costa is single, 20-30 µm wide near the base, sharply demarcated from the laminal cells, ceasing below the apex and often producing clusters of rhizoids at back, with ventral epidermal cells narrowly rectangular to linear and dorsal ones oval above and linear below, smooth to bulging, in transverse section terete to lunate, flat adaxially and convex abaxially, composed of two-three layers of substereid and stereid cells. The laminal cells are unistratose, occasionally with bistratose patches in the apical portion of the leaf, and they are practically homogeneous throughout the lamina. The upper cells are oval to rounded, 5–7  $\mu$ m wide with incrassate walls and they are mostly mammillose and distinctly bulging on both surfaces on young leaves but becoming smooth or only slightly bulging with age. Median and lower leaf cells are somewhat larger, rounded to elliptical 6-8 µm wide, 7-10 µm long, and only a few basal juxtacostal cells are short rectangular (6-8 µm long) to elongate elliptical (15-20 µm long). They are distinctly bulging also on old leaves, giving both leaf surfaces a papillose appearance when viewed under a microscope, but leaf cross sections reveal that the cells are only mammillose, not truly papillose. The plants from Îles Kerguelen are entirely sterile and no sexual organs have been observed.



Fig. 1 *Macrocoma tenue* subsp. *tenue*. (A) Habit. (B) Portion of branches. (C–E) Stem leaves. (F) Branch leaf. (G) Apical cells. (H) Midleaf cells. (I) Basal leaf cells. All from Ochyra 3894/06 (KRAM). Scale bars: 0.5 cm (A), 0.25 cm (B),  $100 \mu \text{m}$  (C–F), and  $50 \mu \text{m}$  (G–I).

#### Specimens examined

**Îles Kerguelen.** Grande Terre, Peninsule Courbet, Val Studer: about 2 km southeast of the southern end of Lac Supérieur, on the right side of Rivière du Sud, 200 m southwest of the large stream going down from Plateau du Tussok, lat. 49°17'38.1" S, long. 70°04'33.1" E; alt. ca. 70 m; forming extensive monospecific mats tightly appressed to an exposed and insolated basalt rock face about 1 m above the highest water level in the river, but often sprinkled and splashed with water, occasionally with an admixture of shoots of *Catagonium nitens* at the edges of mats; December 29, 2006, leg. R. Ochyra 3894/06 (with Ch. Brumbt) (KRAM); same locality, on large basalt block on the river bank on thin soil covering rock, forming large low patches in dry and sunny site, with some scattered shoots of *Bucklandiella pachydictyon* as admixture; December 29, 2006, leg. R. Ochyra 3892/06 (with Ch. Brumbt) (KRAM).

# Discussion

# Taxonomic treatment

*Macrocoma tenue* is the most widespread species of the genus, occurring on all continents except for Europe and Antarctica (Fig. 2). In practice, its geographical range delimits that of the genus which is highly disjunctive and dissected, covering mainly tropical, subtropical, and warm temperate regions of the New and Old Worlds as well as Australasia. Within its wide pancontinental area of occurrence, *M. tenue* exhibits a remarkable variation, which has been the subject of over a dozen new species descriptions. They have been carefully taxonomically assessed and their names have been reduced to synonymy [109,110].

A detailed study of the morphological variation of the populations of *Macrocoma tenue* from all centers of its occurrence, including statistical analyses, led Vitt [112] to recognize two subspecies. The type subspecies is restricted to Africa and East African Indian Ocean islands, southeastern Australia, and New Zealand and it is generally



**Fig. 2** Distribution map for *Macrocoma tenue* subsp. *tenue* (black) and subsp. *sullivantii* (red). A new locality in Îles Kerguelen marked with a star.

characterized by having shorter leaves. They are 0.84-1.13 (mean 0.95), 0.98-1.11 (mean 1.04) and 0.75-1.00 (mean 0.87) mm long, respectively, in the South African, Australian, and New Zealand populations. Additionally, the New Zealand and African populations have shorter apical leaf cells, respectively, 6.47 and  $6.83 \mu$ m on average, and this is obviously correlated with their larger number in the leaf apex, over 14 on average on a length of 50  $\mu$ m down from the leaf tip. In general, the type subspecies of *M. tenue* is characterized by small, short, and narrow leaves, mostly with blunt and incurved apices and homogeneous cells between costa and margin, although the plants from Australia are variable in these traits and morphologically intergrade with the New World populations which belong to the second subspecies, *M. tenue* subsp. *sullivantii* (Müll. Hal.) Vitt.

In the latter subspecies, the leaf length extends from 0.84–1.04 (mean 0.97) mm in the Japanese populations to 0.99-1.54 (mean 1.2) mm in the populations from southwestern Mexico in North America. Except for Japanese populations, the leaves of this subspecies exceed 1.05 mm on average in all other regions of its occurrence including the Hawaiian Islands, Southern India, China, Socotra [116], South America, Mexico, and North Carolina in North America. Likewise, the apical leaf cells are longer in these populations and their length on average ranges from 7.28 µm in the Hawaiian to 8.19 µm in the Mexican populations. The only exceptions are the populations from North Carolina, which are intermediate between the New Zealand and African ones with regard to this character and have an average size of 6.78 µm. The larger size of apical cells in subsp. sullivantii results in the smaller number of cells on a length of 50 µm down from the leaf tip, which ranges, on average, from 13.4 cells in the populations from North Carolina to 9.47 cells in the Mexican plants. The geographical range of M. tenue covers the Americas, Asia, and the Hawaiian Islands in Oceania, and this distribution pattern is similar to that of Bucklandiella subsecunda (Harv.) Bedn.-Ochyra & Ochyra, especially in continental Asia and, additionally, it also covers sub-Saharan Africa [117].

The populations of *Macrocoma tenue* from Îles Kerguelen perfectly match the concept of the type subspecies. The branch leaves are exceptionally small, 0.7–0.8 mm long, and the stem leaves are somewhat longer, to 0.9 mm, and they appear to be the smallest ones in this species. In addition, they have bluntly acute and incurved leaf apices and uniform and small distal laminal cells.

# Phytogeographical considerations

Discovery of *Macrocoma tenue* subsp. tenue in Îles Kerguelen represents a major range extension of this species and the first record of the genus *Macrocoma* in the southern polar regions (Fig. 2). Îles Kerguelen are an archipelago situated in the South Indian Ocean and comprising one major island, Grande Terre, several minor islands, and about 300 islets, rocks, and outliers, remnants of a submerged microcontinent which emerged above sea level by a series of volcanic eruptions associated with the Kerguelen hotspot over the last 115 Ma and which formed the Kerguelen Plateau [118–123]. Exposed basalt rocks date from 29 to 24 Ma [124]. The first eruptions took place near to the junction of the Australian, Indian, and Antarctic plates and the sedimentary rocks of Îles Kerguelen are similar to those found in Australia and India indicating they were all once connected as part of ancient Gondwana [125]. The central plateau was raised above sea level in the Upper Cretaceous and supported a diverse flora for most of the Paleogene and Neogene [125,126].

Climate change is a major impulsive force of population extinctions. During glacial maxima, many taxa retreat from the cooling poles into lower-latitude refugia and subsequently high-latitude habitats can be recolonized by highly dispersive taxa during climate warming in the interglacial periods. Palaeoecological data are still scarce for antarctic and subantarctic islands [127–131]. In the case of Îles Kerguelen, there is remarkably little information on the Quaternary glacial history of this archipelago [131–134]. Some early studies [135–137] suggest that during the Last Glacial Maximum (LGM) glaciation was limited but, in contrast, Hall [138] stated that there may have been a more extensive ice cover during the LGM, except in areas below about 200 m above the present sea level which were likely to have been ice-free. A major question is whether the complete flora of the archipelago, having survived the climatic deterioration

of the latest Pliocene to earliest Pleistocene, could have become entirely extirpated by the late Pleistocene, as suggested by Philippe et al. [139].

Occurrence of *Macrocoma tenue* subsp. *tenue* in Îles Kerguelen may be explained either by its pre-Pleistocene presence in this archipelago and survival of the glacial epoch in situ or as a recent introduction after the Pleistocene glaciation via aerial long-distance transport. A potential source for the origin of the subantarctic populations may be South African and New Zealand localities of this taxon. The African localities are situated about 3,750 km north-northwest of Îles Kerguelen and the prevailing westerly winds are an excellent dispersal vehicle for plants and animals in the Southern Hemisphere [140] and most cases of amphiatlantic distribution patterns can be explained in this way. The theory that long-distance dispersal of moss spores plays an important role in the establishment of the present-day ranges was confirmed by experimental studies [141].

An Afro-American distribution is being demonstrated for an increasingly large number of moss species, primarily tropical lowland and montane species [142–149], but this type of distribution includes also a relatively small group of south-temperate cool-adapted moss species [39,43,76,150–152]. However, South Africa is north of the main track of westerly winds and there are only a very few moss taxa which occur in South Africa and on Îles Kerguelen, for example *Vittia pachyloma* (Mont.) Ochyra [153] and *Bucklandiella lamprocarpa* (Müll. Hal.) Bedn.-Ochyra & Ochyra [154,155] and the main center of their occurrence is in southern South America [153,156,157]. Moreover, the South African and Kerguelen populations of *Macrocoma tenue* differ markedly in leaf size [112], whereas the Kerguelen populations are most alike those from New Zealand. Interestingly, as stated above, the Australian populations have markedly larger leaves, 1.04 mm on average and deviate markedly in this character from those in the New Zealand populations. The New Zealand–Îles Kerguelen distribution pattern is exceedingly rare and the only good example amongst mosses is the distribution of *Ditrichum strictum* (Hook. f. & Wilson) Hampe [52].

When reconstructing a possible evolutionary history of the *Macrocoma tenue* complex, Vitt [112] suggested that *Macromitrium*, as a collective genus, evolved in Gondwana, after the split of the supercontinent Pangea but before the break-up of the Gondwana continental mass, about 150 Ma in the Upper Jurassic. The present geographical distribution of *M. tenue*, especially its discovery in Îles Kerguelen (Fig. 2), supports this hypothesis and complements the entire evolutionary puzzle. The species could have evolved early in Gondwana, possibly in the Lower Jurassic, from where it reached Îles Kerguelen. These land masses, being above sea level at the time of the earliest angiosperm and moss radiations and with a palaeo-position off northeastern India, are suggested to have been a crucial corridor for early angiosperm and moss dispersal to southern high latitudes [125]. Acceptance of this hypothesis implies that *M. tenue* is an ancient taxon which survived or evolved in situ in Îles Kerguelen following the break-up of Gondwana.

This scenario may inferentially be confirmed by the history of *Didymodon gelidus* Cardot. This species has long been considered to be an Antarctic endemic [158]. Although later it lost the status of an independent species because it was merged with the Holarctic *D. brachyphyllus* (Sull.) R. H. Zander [159,160], thorough morphological studies have restored this previous status of a distinct species [8] which has optimum occurrence in the Antarctic, with only occasional localities on South Georgia [18] and in Îles Kerguelen [161] in the Subantarctic. This distribution pattern clearly shows that *D. gelidus* probably evolved in Gondwana before its break-up from where it reached Îles Kerguelen. It is especially so, because this species is highly isolated taxonomically and its only closest relative, *D. cardotii* (Dusén) R. H. Zander, occurs in Patagonia [8].

The occurrence of a number of endemic species on these islands further supports this hypothesis. Îles Kerguelen are an important center of endemism, perhaps not in the number of endemic taxa but their taxonomic position. The two monotypic vascular plant genera, *Lyallia* Hook. f. (with *L. kerguelensis* Hook. f.) and *Pringlea* R. Br. (with *P. antiscorbutica* R. Br.), are highly isolated taxa [162,163] and are emblematic for the Kerguelen Biogeographical Province. The former is the only phanerogam strictly endemic to Îles Kerguelen, whereas the latter is endemic to the whole province, but it apparently evolved in Îles Kerguelen from whence it spread to other archipelagoes and islands of this province, including Îles Crozet, the Prince Edward Islands, and Heard

Island. The case of *Lyallia* is particularly meaningful in the context of the close similarity of Kerguelen and New Zealand populations of *M. tenue* because its only close relative is the endemic bitypic genus *Hectorella* Hook. f. from New Zealand.

Kerguelen Biogeographical Province, with Îles Kerguelen being the largest and oldest archipelago of this region, is a remarkable center of moss endemism in the Subantarctic. It appears to be a center of diversity of the genus *Hymenoloma* Dusén, with three endemic species, *H. dryptodontoides* (Müll. Hal.) Ochyra, *H. tortifolia* (Hook. f. & Wilson) Ochyra, and *H. insulare* (Mitt.) Ochyra [73]. Additional endemic species of moss include *Bucklandiella ochracea* (Müll. Hal.) Bedn.-Ochyra & Ochyra, *Ditrichum subaustrale* Broth., *Valdonia microcarpa* (Mitt.) Ochyra, *Campylopus subnitens* Kaal., *C. austrostramineus* Thér., *Hennediella marginata* (Hook. f. & Wilson) R. H. Zander, *Syntrichia christophei* Ochyra & R. H. Zander, *Willia calobolax* (Müll. Hal.) Lightowlers, *Schistidium serratomucronatum* (Müll. Hal.) Ochyra, *S. chrysoneuron* (Müll. Hal.) Ochyra, *Bryum orthotheciellae* Müll. Hal., *B. kerguelense* Mitt., *Dicranella gremmenii* Ochyra, *Distichophyllum imbricatum* Mitt., *D. fasciculatum* Mitt., *Muelleriella atrata* (Mitt.) Vitt, and *M. crassifolia* (Hook. f. & Wilson) Dusén subsp. *acuta* (Müll. Hal.) Vitt.

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