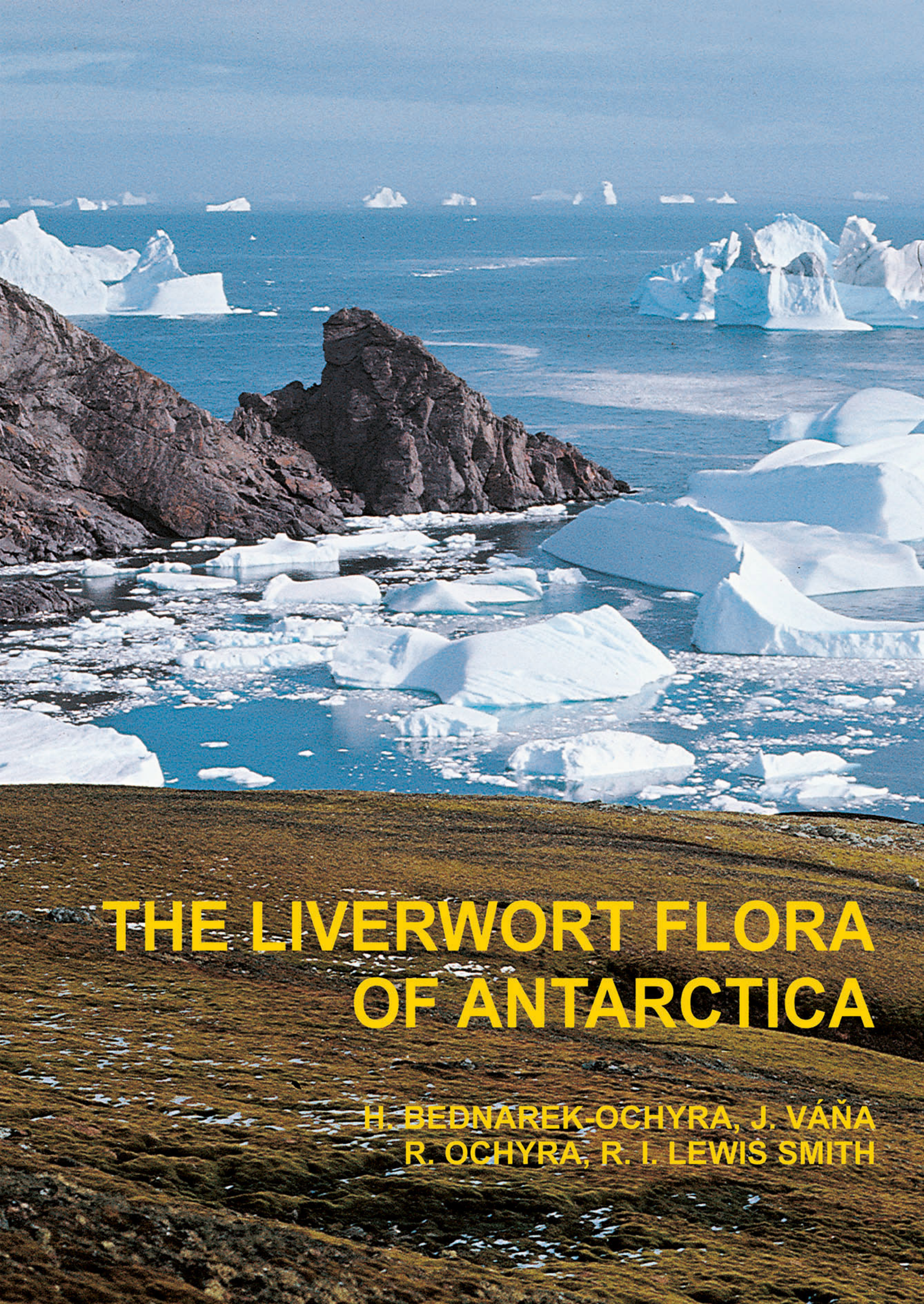

THE LIVERWORT FLORA OF ANTARCTICA

H. BEDNAREK-OCHYRA, J. VÁŇA
R. OCHYRA, R. I. LEWIS SMITH

THE LIVERWORT FLORA
OF ANTARCTICA

FRONTISPIECE: *Anthelia juratzkana*

THE LIVERWORT FLORA
OF ANTARCTICA

HALINA BEDNAREK-OCHYRA, JIŘÍ VÁŇA,
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Cracow, 2000

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Dedicated to
Riclef Grolle
in recognition of his valuable
contribution to the taxonomy and biogeography
of austral liverworts

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Taxonomic and nomenclatural novelties

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New lectotype:

Cephaloziella antarctica Douin	81

New name:

Hygrolembidium R. M. Schust. subgen. *Hygrobiellopsis* R. M. Schust. *ex* Bedn.-Ochyra *et al.*	56

Foreword

There are few comprehensive treatments of the bryoflora of entire continents. Although the bryoflora, and especially the liverwort flora, of Antarctica has very few species, it has remained the least known continent from this respect until now. There are three reasons for this. Firstly, field work and collecting in the harsh conditions on the coldest and most inhospitable continent is possible only within the framework of well-organised national expeditions. Secondly, the habitats available for liverworts are very scattered, are restricted to a very small proportion of the land surface and are accessible during a relatively short period of the year. Thirdly, although records from the continent and its offshore islands have been accumulating since the end of the nineteenth century, the level of taxonomic knowledge and interest in the biodiversity of the Antarctic biome has been minimal until very recently. Only now is it possible to prepare a comprehensive synthesis.

The expertise of the Authors has contributed significantly to the knowledge of the Antarctic hepatic flora and, in this *magnum opus*, they have critically evaluated almost all available specimens and data, both taxonomically and biogeographically. The user-friendly practical keys, detailed taxonomic descriptions with precise and artistic illustrations, together with associated reproductive, ecological and distributional (both regional and global) information, all contribute to providing a comprehensive account of each species. I am convinced that both the bryological community and non-specialist naturalists will benefit greatly from this very detailed and easily manageable monograph. I personally wish to congratulate the Authors on the occasion of the publication of their meticulous work resulting in this landmark in hepaticology.

Eger, 11 September 2000 Tamás Pócs

Preface

The liverworts, or hepatics, are one of the major components of the terrestrial vegetation in Antarctica. They are usually less common and less prominent than mosses and are often concealed within moss turfs, cushions and mats. Similarly, diversity of the liverworts is about one quarter that of mosses. Despite their inconspicuousness these plants have often been collected, both selectively and casually, during bryological surveys. Over several decades collections of liverworts have been deposited in various world herbaria, forming a good basis for their comprehensive taxonomic, ecological and phytogeographical treatment. This Flora will be of considerable value to scientists undertaking research on the terrestrial vegetation in this region, as an aid to the identification of species, to ecological analysis, and to understanding the biogeographic relationships of the Antarctic flora both in a regional and in a global context.

Much of the background field work for this Flora was undertaken over almost 40 years by RILS throughout the maritime Antarctic and at some continental Antarctic sites. In addition, RO collected liverworts intensively on King George Island in 1979–1980. Resulting from these field studies, frequent reference to liverworts has been made in ecological accounts. This liverwort Flora began in parallel with the Antarctic Moss Flora (Ochyra *et al.*, 1997; Lewis Smith *et al.*, 1998) in the mid-1990s.

When the present book goes to press, on 1st September 2000, it will be exactly a century to the day since the publication of the first account on Antarctic liverworts by F. Stephani. This was the results of his studies on the collection brought back from the Antarctic Peninsula region by the Belgian Antarctic Expedition. Thus, the publication of the present volume has also a symbolic significance. While Antarctic hepaticology was very slow to develop, great advances were made in their discovery and accurate identification during the last decade of the twentieth century.

Plant taxonomy is now entering a new era in which DNA sequencing and other molecular techniques will almost certainly revolutionize biological systematics. For the present, however, we must rely on sound classical treatment to enable identification of species. Therefore, we hope that the present work, despite some shortcomings, will be a reliable and valuable starting point for modern studies. We expect that, in due course, the application of molecular techniques will help to resolve critical problems which cannot be overcome by traditional methods, and provide answers to questions which we could not satisfactorily answer because of the limitations of the traditional methods, e.g. the problem of identification of taxa in the *Cephaloziella exiliflora* complex, or the identity of the plants presently named with reservation *Lophozia* cf. *groenlandica*.

Completion of this Flora and resolving some taxonomic problems would not have been possible without the kind assistance of several colleagues. We are particularly grateful to Riclef Grolle (Jena), John J. Engel (Chicago) and Rudolf M. Schuster (Hadley) for valuable information regarding certain specimens and taxonomic concepts. We cordially thank also Directors, Curators and owners of the private herbaria cited in the text for kindly allowing us to study specimens. In particular, we are thankful to Helen J. Peat (BAS, Cambridge) for providing easy access to the large bryological collection deposited in the British Antarctic Survey (AAS). We are grateful to D. J. Cantrill for information on fossil hepatics in Antarctica, and to K. K. Newsham for information on UV-B-induced pigments in *Cephaloziella varians*. Special thanks are also due to Katarzyna Biłyk for generating distribution maps and various technical assistance during completing this research. Many collegues served us with rare and not easily accessible bryological literature and we thank the assistance of William R. Buck (New York), Lars Hedenäs (Stockholm), Denis Lamy (Paris), Brian O'Shea (London), Sinikka Piippo (Helsinki), Herman Stieperaere (Meise) and Hans-Joachim Zündorf (Jena).

We wish to express our sincere gratitude to the Institute of Botany of the Polish Academy of Sciences (HBO, RO), Institute of Botany of Charles University (JV) and the British Antarctic Survey (RILS), without whose support this work would not have been possible. In particular, the project has gained financial support from the Polish State Committee for Scientific Research through grant No 6P04C 038 12 for HBO. The Institute of Botany of the Polish Academy of Sciences provided the financial support for publication of this book which is gratefully acknowledged. Finally, we are indebted to Kazimierz Karczmarz (Lublin), Tamás Pócs (Eger) and Jerzy Szweykowski (Poznań) for critically reading the text and suggesting improvements.

Kraków – Prague – Cambridge
21 August 2000

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Chapter 1

INTRODUCTION

The Antarctic is unique amongst the biomes of the world in having a terrestrial biota comprising almost exclusively lower organisms (microorganisms, fungi, lichenised fungi, algae, bryophytes, invertebrates). There are only two native phanerogams (Antarctic hairgrass, *Deschampsia antarctica* Desv., and Antarctic pearlwort, *Colobanthus quitensis* (Kunth) Bartl.), and these occur only on the islands of the Scotia Ridge and along the western coast of the Antarctic Peninsula (Lewis Smith, 1984*a*, 1996; Lewis Smith & Poncet, 1985, 1987). While the greatest diversity of mosses and lichens also occurs in this region, liverworts play only a minor role in the flora and vegetation, and these are reduced to a single species in continental Antarctica.

Increasing scientific interest in Antarctica since about 1980 has changed perceptions of the continent. Long regarded as being of little scientific significance, Antarctica is now seen as commanding a key position in many research disciplines. In addition, growing tourism, interest in global biodiversity and a need for more active conservation have led to a recognition that modern identification manuals are essential for Antarctica.

This is the first comprehensive and critical taxonomic account of the liverworts of the Antarctic biome. It will contribute to a better understanding of the flora, provide more accurate distributional and ecological data and permit more reliable assessments of biogeographical affinities, origins, dispersal routes and evolutionary trends.

The objective of this work is to provide a comprehensive account of the liverworts of Antarctica based on critical assessment of specimens in several of the world's major herbaria and on ecological data for habitats and communities. Individual taxa have been compared with type specimens wherever possible, and with material from other parts of the world.

BIOGEOGRAPHIC ZONES

The Antarctic (Fig. 1) is defined geopolitically, for the purposes of the internationally adopted Antarctic Treaty (Heap, 1994), as all land and adjoining ice shelves south of latitude 60^{o}S (Article VI). In accordance with the Antarctic Treaty, there are no national territorial claims recognised within this region, and all pre-Antarctic Treaty claims, often still indicated on maps, have been waived (Anonymous, 1961). Although this landmass covers about 14 million km^2 (about 1.5 times the area of Europe), only ca 0.3% is ice-free in summer (Fox & Cooper, 1994), and

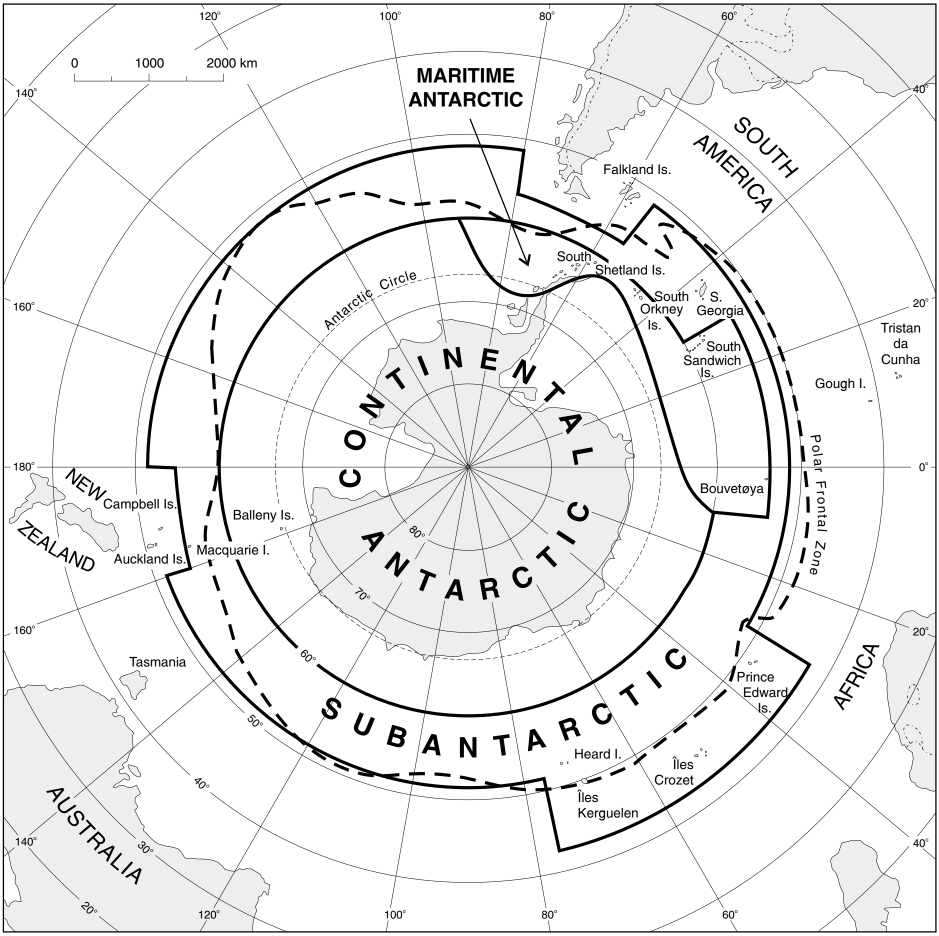


FIGURE 1. Antarctica, the Southern Ocean and subantarctic islands, showing the Polar Frontal Zone (broken line, also known as the Antarctic Convergence in the older literature) and subdivisions of the Antarctic into biogeographic zones (after Ochyra, 1998).

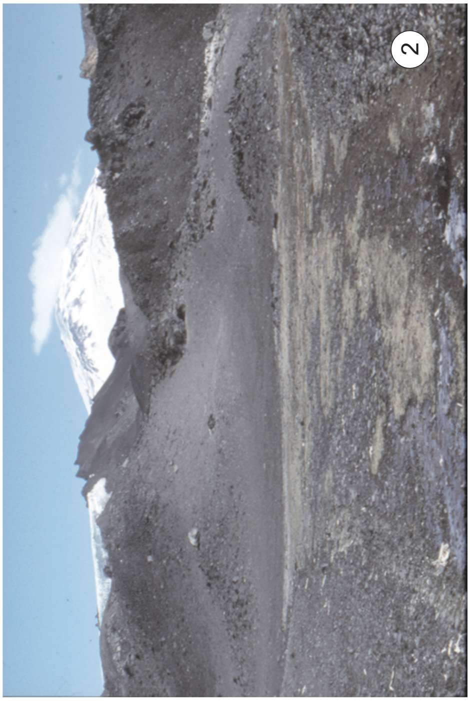
much of that is inaccessible precipitous inland rock. The South Sandwich Islands, lying north of 60^{o}S, and therefore excluded from the Antarctic Treaty Area, are a dependent territory of the United Kingdom situated on the Scotia Ridge, a submarine mountain range extending eastwards from the Andes Mountains in southern South America to Trinity Peninsula, Graham Land, in the northern Antarctic Peninsula. Also on this arc rise the archipelagoes of the South Orkney and South Shetland Islands, as well as the subantarctic island of South Georgia to the north. Bouvetøya, a Norwegian territory, lies in the mid-South Atlantic Ocean and is also outwith the Antarctic Treaty Area.

Biogeographically, the Antarctic biome may be divided into zones which correspond to distinct climatic (and botanical) regions. These broadly latitudinal zones have been variously defined in several phytogeographic accounts (e.g. Skottsberg, 1912, 1960; Greene, 1964*a*; Wace, 1960, 1965, 1969; Godley, 1960; Holdgate, 1964, 1967; Lewis Smith, 1984*a*; Pickard & Seppelt, 1984; Longton, 1988). Greene (1968) divided the “Antarctic botanical zone” (i.e. all land south of lat. 60^{o}S, together with the South Sandwich Islands and Bouvetøya) into six longitudinal sectors, named after predominant geographic features. These are: Maud (from 30^{o}W to 30^{o}E), Enderby (30–90^{o}E), Wilkes (90–150^{o}E), Ross (150^{o}E–150^{o}W, Byrd (150–90^{o}W), Scotia (90–30^{o}W). The system adopted here (Table 1) is taken from Lewis Smith (1984*a*).

Continental Antarctic zone

Continental Antarctica (Fig. 2) includes all of the continent and its offshore islands (including southern Alexander Island), but excluding the western side of the Antarctic Peninsula north of 70^{o}S. Because the climate of the east coast of the Antarctic Peninsula is much colder and drier than the west side, the former region is considered to be transitional between maritime and continental Antarctic. Within this region are isolated small areas with a relatively diverse terrestrial biota (e.g. on Joinville Island, Dundee Island, Vega Island, James Ross Island, and at Seal Nunataks and around Cabinet Inlet); parts of eastern Alexander Island (attached to the south-western Antarctic Peninsula by the George VI Sound Ice Shelf) and Charcot Island to the west of Alexander Island are also within this transitional zone.

Parts of the coastal region of Eights Coast (especially Thurston Island) probably have the most diverse biota in continental Antarctica, and represent an important transition between those of the tectonically distinct plates of East and West Antarctica. Although no liverworts have yet been reported from this region, it is probable that one or two species will be found here. Continental Antarctica may be divided into coastal, slope and inland provinces, but one species of liverwort occurs only in a few of the more climatically favourable coastal areas with adequate free water during the short summer.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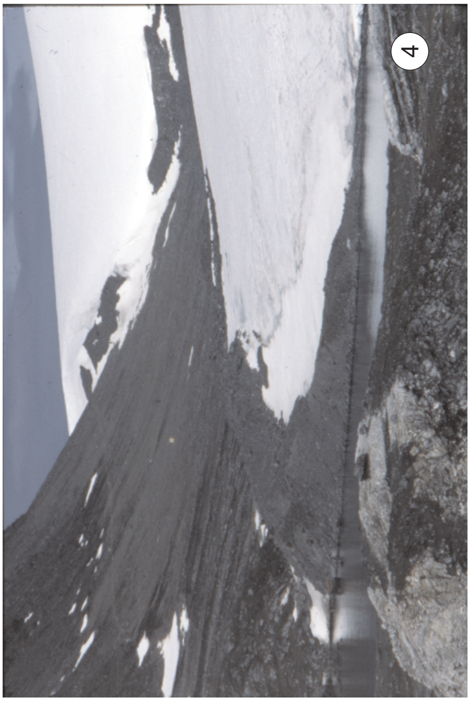
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Maritime Antarctic zone

The maritime Antarctic (Figs 5–9) comprises the South Sandwich (Figs 3, 13–14), South Orkney (4–6, 16) and South Shetland Islands, and the west coast of the Antarctic Peninsula (Figs 7–9) and its offshore islands, to about 70°S (in southern Marguerite Bay). Floristically, this biological zone possesses the two vascular plants (to about 68°30'S, Lewis Smith & Poncet, 1987) and has a relatively diverse bryophyte and lichen flora (Gimingham & Lewis Smith, 1970; Lewis Smith, 1984*a*, 1996). It also includes the climatically similar but extremely isolated small glacierised island Bouvetøya (southern Atlantic Ocean) which has an entirely cryptogamic biota. The region may be divided into northern and southern sub-zones or provinces.

CLIMATE

Unlike the Arctic biome, the Antarctic has very cold summers which is a major factor determining the survival of terrestrial biota in the south polar regions. There is a very wide latitudinal range of climatic conditions, especially of temperature, precipitation and daylength, throughout the Antarctic (see Table 1). This is most critical along the north-south gradient of the maritime Antarctic, which is the most floristically diverse region.

Within the Antarctic, air temperatures at lowland coastal sites often exceed 0°C during the day in the short summer (generally considered as December to February), but typically drop below freezing at night, thereby frequently subjecting the

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FIGURES 2–5. **2.** Extensive stand of *Bryum subrotundifolium* with occasional *Cephaloziella varians* in a snow melt seepage area; in the background is the summit of the volcano Mt. Melbourne (2733 m) where *C. varians* occurs on the geothermally heated Cryptogam Ridge, the only Specially Protected Area site in Antarctica specifically designated to prevent disturbance of a liverwort. Victoria Land, Edmonson Point, *ca* 15–20 m alt. **3**. Hepatic-rich community around a former steam-emitting fissure at *ca* 10 m alt. South Sandwich Is., Saunders I., Blackstone Plain looking east to Yellowstone Crags in background. **4**. Deglaciated Moraine Valley showing the trim-line (upper left) on the ice-free slope of Rusty Bluff representing the point to which the Orwell Glacier (right) reached during the 18th–19th centuries. The persistent vegetation above this line comprises a considerable diversity of bryophytes, including an abundance of several liverworts, notably *Anthelia juratzkana*, *Barbilophozia hatcheri*, *Cephaloziella varians*, *Herzogobryum teres*, *Hygrolembidium isophyllum*, *Lophozia excisa*, *Pachyglossa dissitifolia*, and the very rare *Lophozia* cf. *groenlandica*. In the foreground are outcrops of limestone (white rock of Marble Knolls) which support a completely different cryptogamic flora to that of the quartz-mica schist of Moraine Valley; *Marchantia berteroana* is frequent on the calcareous soil. South Orkney Is., Signy I., 0–50 m alt. **5**. East-facing scree slopes and cliffs below Rusty Bluff (220 m); green areas are mainly *Chorisodontium aciphyllum-Polytrichum strictum* turf. Dark areas are wet rock where about two-thirds of the Antarctic (excluding South Sandwich Is.) liverwort flora occurs, including the elusive *Cephaloziella hispidissima*, *Metzgeria decipiens* and *Pachyglossa fissa*. South Orkney Is., Signy I., Paal Harbour, 0–220 m alt. [Photos 2, 4 and 5 by R. I. Lewis Smith; 3 by P. Convey.]


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biota to a diurnal freeze-thaw cycle during its most physiologically active period. Winter temperatures rarely exceed 0°C and are generally far below freezing point but, since the biota is usually covered by an insulating blanket of snow, it remains dormant and unaffected. Extreme air temperatures during summer may very briefly (a few hours at the most) reach about 10°C in the northern maritime Antarctic, and 5°C in the southern maritime Antarctic and coastal continental Antarctica. The approximate mean summer and annual air temperatures for most regions of the Antarctic where liverworts occur are given in Table 2. At many coastal stations with long-term meteorological records there has been a steady increase in air temperature of between 0.02 and 0.05°C per year since the 1950s (King & Turner, 1997).

Precipitation in the maritime Antarctic is frequently as rain during summer, but snow can fall at any time of the year; there is deep snow cover for up to eight months, even at sea level. Farther south, rain becomes increasingly scarce, and winter snow cover can last for eight to ten months of the year. Rainfall equivalent ranges from about 350–500 mm in the northern maritime Antarctic to 50–100 mm in the southern Antarctic Peninsula and much of coastal continental Antarctica. Where precipitation is less than this, free water is very sporadic and liverworts are unable to survive.

GEOLOGY

In general, Antarctic liverworts are not strongly influenced by geochemistry; unlike mosses, there is no exclusive group of species occurring on highly calcareous rock (e.g. on Signy Island, South Orkney Islands). The following broad account is taken from Tingey (1991) and Lewis Smith (1993*a*).

Antarctica consists of two geological provinces: the ancient continental shield of East or Greater Antarctica, and the mainly magmatic arc of West or Lesser Antarctica. These are geographically separated by the 3500 km long Transantarctic Mountains. East Antarctica is composed largely of crystalline basement rocks

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FIGURES 6–9. **6**. Extensive moss turf community formed by *Chorisodontium aciphyllum* and *Polytrichum strictum*, usually containing an abundance of *Barbilophozia hatcheri*, *Cephaloziella varians*, *Lophozia excisa* and very rarely *Lepidozia chordulifera*. South Orkney Is., Signy I., Moss Braes, *ca* 50–75 m alt. **7**. Diverse bryophyte community on moist north-facing hillside, with frequent liverworts (*Barbilophozia hatcheri*, *Cephaloziella varians*, *Lophozia excisa, Marchantia berteroana*). Danco Coast, Cierva Point, *ca* 35 m alt. **8**. The north-west-facing rocky slopes of Cape Tuxen, on the mid-west coast of the Antarctic Peninsula, has a diverse bryophyte vegetation, including several species of liverworts including *Herzogobryum teres*, *Metzgeria decipiens*, and *Pachyglossa dissitifolia*, Graham Coast, 0–500 m. **9**. Extensive swards of *Deschampsia antarctica* with associated bryophytes including *Cephaloziella varians*, *Barbilophozia hatcheri* and *Lophozia excisa*. Marguerite Bay, Léonie I., *ca* 25–30 m alt. [Photos 6, 8 and 9 by R. I. Lewis Smith; 7 by G. Mataloni.]

TABLE 1. Geobotanical zones of the Antarctic (modified from Lewis Smith, 1984*a*).

Localities	Province	Region	Climatic features	Biotic features
Bouvetøya, South Sandwich, South Orkney and South Shetland Islands, west coast of Antarctic Peninsula *ca* 68°S.	Maritime Antarctic	Northern	Cold moist maritime climate, mean monthly temperatures >0°C for 3–4 months in summer but rarely <-10 to -12°C in winter; precipitation 350–500 mm per annum with much as rain in summer. Snow-free period (SFP) *ca* 15–20 weeks.	Fellfield dominated by cryptogams but including small closed stands of *Deschampsia antarctica* and associated *Colobanthus quitensis*; locally diverse flora near coast; mosses form closed stands in wetter habitats, locally accumulating peat; liverworts frequent; lichens predominate in exposed drier situations and inland; snow algae and macrofungi frequent in summer. Abundant marine bird and mammal fauna; substantial invertebrate fauna dominated by mites and springtails and including two native higher insects (Diptera).
West coast of Antarctic Peninsula from *ca* 68–70°S, and offshore islands; also north-east coast to *ca* 64°S.	Maritime Antarctic	Southern	Cold dry maritime climate, mean monthly temperatures >0°C for 1–3 months in summer but rarely < -15°C in winter; precipitation <350 mm water equivalent with occasional rain. SFP *ca* 12–18 weeks.	As for Northern Region but cryptogamic diversity less and closed stands infrequent; two phanerogams relatively common and one Diptera occasional at west coast sites only; moss peat accumulation minimal.
Coastal fringe of East Antarctica and West Antarctica south of 70°S, and east coast of Antarctic Peninsula south of 64°S; includes Peter I Øy, Scott and Balleny Islands	Continental Antarctic	Coastal	Cold arid climate, mean monthly temperatures >0°C for 0–2 months in summer; winter monthly means from -5 to -25°C but some maritime influence narrowing temperature range; precipitation *ca* 100–150 mm water equivalent; rain very rare. SFP *ca* 10–15 weeks.	Semi-desert with moss and alga vegetation on moist ahumic soil; bryophyte diversity very low; lichens relatively diverse, locally forming extensive stands; snow algae occasional in some localities; cyanobacteria abundant in wet sites. Invertebrates locally diverse and abundant. Seabird colonies locally frequent and large; marine mammals abundant offshore.
Mountain and glacier zone inland from coast encircling the central ice plateau; includes isolated nunataks in ice plateau and ice-free “dry valleys”.	Continental Antarctic	Slope	Extremely cold and arid climate, mean monthly temperatures <-5°C in summer and <-30°C in winter; precipitation <100 mm water equivalent; no rain. 1–3 months continual daylight in summer.	Desert with very occasional discontinuous lichen stands; mosses very rare; most vegetation associated with snow petrel colonies and microclimatically favourable oases. Some mites and nematodes; springtails very rare. Endolithic microorganisms in suitable sandstones.
Continental interior, generally >2000 m altitude.	Continental Antarctic	Ice Plateau	Extreme continental climate, all mean monthly temperatures <-15°C, <-50°C in winter; slight precipitation. Daylight as Slope Province.	Macroscopic life restricted to very occasional lichens, algae and cyanobacteria; some microorganisms. Vagrant birds very rare.

TABLE 2. Approximate mean summer (December–February) and mean annual air temperatures near sea level in the major biogeographic regions of coastal Antarctica from which liverworts have been recorded (data taken from Øvstedal & Lewis Smith, in press; Lewis Smith, 1993*a*; King & Turner, 1997).

Region	Mean temperature (°C)	
	Summer	Year
Maritime Antarctic		
Bouvetøya	1	-2
South Sandwich Islands	1	-2
South Orkney Islands	1	-3 to -4
South Shetland Islands	1 to 2	-2 to -3
North-western Antarctic Peninsula	0 to 1	-4 to -5
Mid-western Antarctic Peninsula	0 to 1	-3 to -4
South-western Antarctic Peninsula	0	-5 to -7
North-eastern Antarctic Peninsula	-2	-9
Mid-eastern Antarctic Peninsula	-3	-10 to -12
South-eastern Antarctic Peninsula	-5	-16 to -20
Alexander Island	-2	-15 to -20
Continental Antarctic		
Wilkes Land	-1	-8 to -9
Princess Elizabeth Land	0 to -1	-10
Northern Victoria Land	-2 to -5	-12 to -15
Southern Victoria Land	-5 to -7	-17 to -20

which are intruded by a variety of igneous rocks. Almost all are Precambrian in age. By contrast, the Transantarctic Mountains contain a variety of sedimentary rocks of mainly Cambrian to Triassic age. The older Cambrian to Ordovician rocks are strongly deformed, whereas the younger Devonian to Triassic sediments of the Beacon Supergroup (Transantarctic Mountains and Prince Charles Mountains) are usually flat-lying. With the exception of limestones in the Cambrian rocks, the whole sedimentary sequence is dominated by sandstones and conglomerates, with less frequent occurrences of shales. In the coastal areas of Victoria Land and Ross Island there are exposures of late Cenozoic basaltic volcanic rocks; these include the active volcanoes of Mt. Erebus, Mt. Melbourne and Mt. Rittmann. Similar rocks are present on the coast at Gaussberg (90°E). The spectacular mountain ranges in Dronning Maud Land are mainly of granitic gneisses, migmatite, charnockite and diorites.

West Antarctica is much younger and more complex than East Antarctica, and geologically related to southern South America and New Zealand. It comprises five crustal blocks or provinces, of which the Antarctic Peninsula is the largest. Most of this province consists of the remnants of a long phase of magmatic arc activity. Metamorphic rocks (schists and gneisses) occur at many places. Most of the rocks forming the Antarctic Peninsula and farther south (e.g. Thurston Island crustal block) consist either of the volcanic and plutonic products of the magmatic activity or of the sedimentary rocks which accumulated in the seas around its margins. From at least Jurassic until early Cenozoic times the volcanism was dominated by andesitic rocks, with lesser amounts of rhyolites and basalts; plutonic rocks include granite, granodiorite, diorite and gabbro. Sedimentary rocks include Late Palaeozoic-Triassic shales and greywackes and Jurassic-Cretaceous fossiliferous marine shales and sandstones. Outcrops of marble (limestone) are frequent on Signy Island, but very rare elsewhere in the Antarctic Peninsula region, e.g. isolated patches on the east coast of Graham Land and south-west coast of Palmer Land; calcareous nodules and concretions occur in some Antarctic Peninsula localities (e.g. James Ross Island). The Ellsworth-Whitmore Mountains crustal block is mainly sedimentary and includes limestones, sandstones and shales of Cambrian to Permian age, which had originally been deposited by rivers or in shallow seas. Late Cenozoic basaltic and other volcanic rocks occur in the James Ross Island area, the South Shetland Islands, the western seaboard of the northern Antarctic Peninsula, Peter I Øy and Marie Byrd Land. The volcano of Deception Island is still active, and there is fumarolic activity here and on some of the South Sandwich Islands and Bouvetøya; all are composed of basalts and lavas.

Chapter 2

HISTORY OF THE HEPATICOLOGICAL INVESTIGATIONS

EARLY EXPLORATION

Besides several casual reports of mosses in the South Shetland Islands during the 1820s and 1830s (Anonymous, 1821; Sherratt, 1821; Eights, 1833; Webster, 1834), bryological exploration of the Antarctic commenced at the small Cockburn Island off the east coast of Trinity Peninsula. On 6 January 1843 J. D. Hooker, assistant surgeon and botanist on James Clark Ross' British Antarctic Expedition of 1839–1843, was the first professional botanist to visit the Antarctic. On this island he collected five species of moss (Hooker, 1847; Wilson & Hooker, 1847) and several lichens, but no liverwort species was discovered. This is perhaps not surprising because Cockburn Island exhibits a relatively small range of habitats and has a cold dry climate unfavourable for many species of moss and liverwort which are widespread elsewhere in the maritime Antarctic, especially along the western coast of the Antarctic Peninsula. The absence of liverworts here was confirmed by Lewis Smith (1993*b*).

For over half a century after Hooker's visit no further bryological collections were made in the Antarctic biome. At the end of the nineteenth century several national expeditions explored the Antarctic and some of them brought back valuable botanical collections. Because liverworts are not prominent constituents of the impoverished Antarctic vegetation, only a few specimens of these plants were collected in the "Heroic Age" of Antarctic exploration and all were from islands adjacent to the northern part of the Antarctic Peninsula.

The Belgian Antarctic Expedition of 1897–1899, under the command of A. de Gerlache de Gomery, was the first to overwinter in the Antarctic. E. Racovitza, naturalist to the expedition, collected three species of liverworts in the Gerlache Strait region of the Danco Coast on the western Antarctic Peninsula. These were identified by Stephani (1901) as *Lophozia hatcheri* (now *Barbilophozia hatcheri*) (Fig. 10), *L. propagulifera* (now *L. excisa*) and *Cephalozia varians* (now *Cephaloziella varians*). These species are now known to be the most widespread liverworts in the Antarctic biome. The material of *C. varians* collected by Racovitza was subsequently described by Douin (1920) as a separate species, *Cephaloziella antarctica* (Fig. 11).

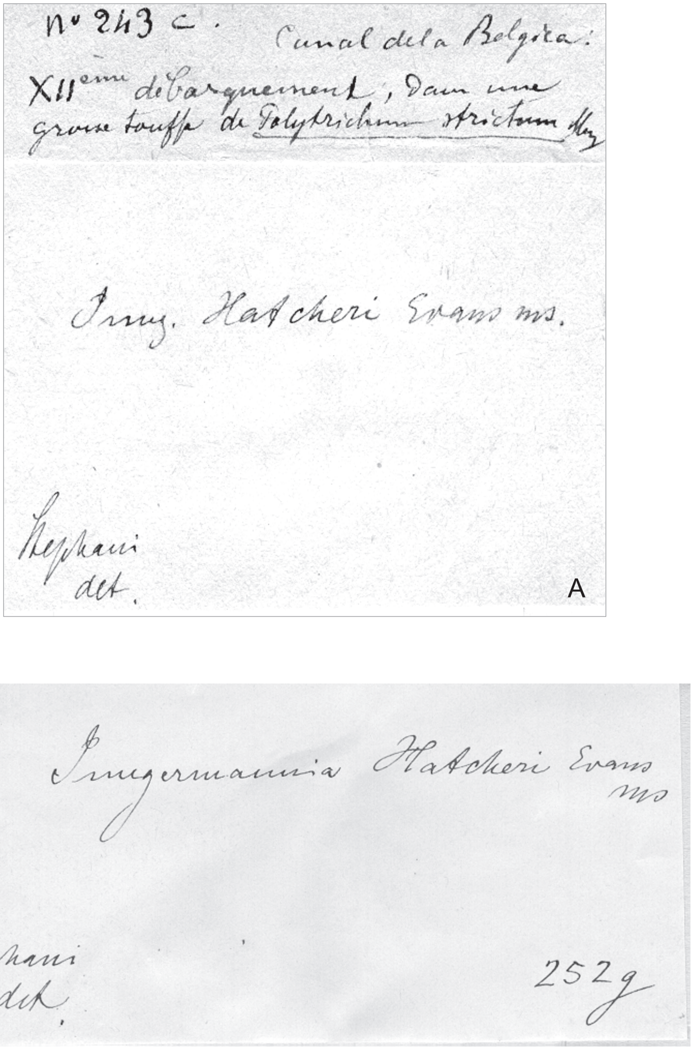
The only other collection of liverworts at this time was made by C. Skottsberg during the Swedish South Polar Expedition of 1901–1903 in the Orléans Strait region of the Davis and Danco Coasts of the western Antarctic Peninsula. These were also identified by Stephani (1905) who recognized four species, namely *Lophozia badia* (now *Cephalozia badia*), *L. propagulifera* (now *L. excisa*) (Fig. 12D), *L. floerkei* (now *Barbilophozia hatcheri*) (Fig. 12A–C) and *Cephalozia cucullifolia* (now *C. badia*), of which the latter was described as a species new to science.

Although several miscellaneous collections of bryophytes were made subsequently in the Antarctic (Ochyra *et al.*, 1998), no new liverworts were determined or reported in the literature for about 60 years. They were generally overlooked, even in areas which today are considered to have the most diverse hepaticoflora such as the South Orkney Islands (Rudmose Brown, 1906). Thus, until the early 1960s, only four species of hepatic had been reported from the Antarctic botanical zone (Steere, 1961) and three of these are the commonest representatives of this plant group.

POST-1960 PERIOD

The International Geophysical Year of 1957–1958 began a new era in the history of exploration and scientific research in Antarctica, with the establishment of many new stations throughout the Antarctic Peninsula and around the continent. During the 1960s there was a rapid increase in the location and nature of biological research. Unlike the early days of Antarctic exploration when collections were seldom made by botanists, post-1960 field research has involved many professional botanists, including bryologists, in studies of the Antarctic flora and vegetation. This resulted in the rapid acquisition of bryological information in this region. Although liverworts are often inconspicuous and play an insignificant role in Antarctic terrestrial ecosystems, since the early 1960s the number of hepatics reported from within the Antarctic botanical zone increased considerably.

Most of these collections were made by scientists of the British Antarctic Survey at many localities throughout the maritime Antarctic, from the South Sandwich



N° 243 c. Canal de la Belgica:
XIIème débarquement, Dans une
grosse touffe de Polytrichum strictum Menz

Jung. Hatcheri Evans ms.

Stephani
det.

Jungermannia Hatcheri Evans
ms

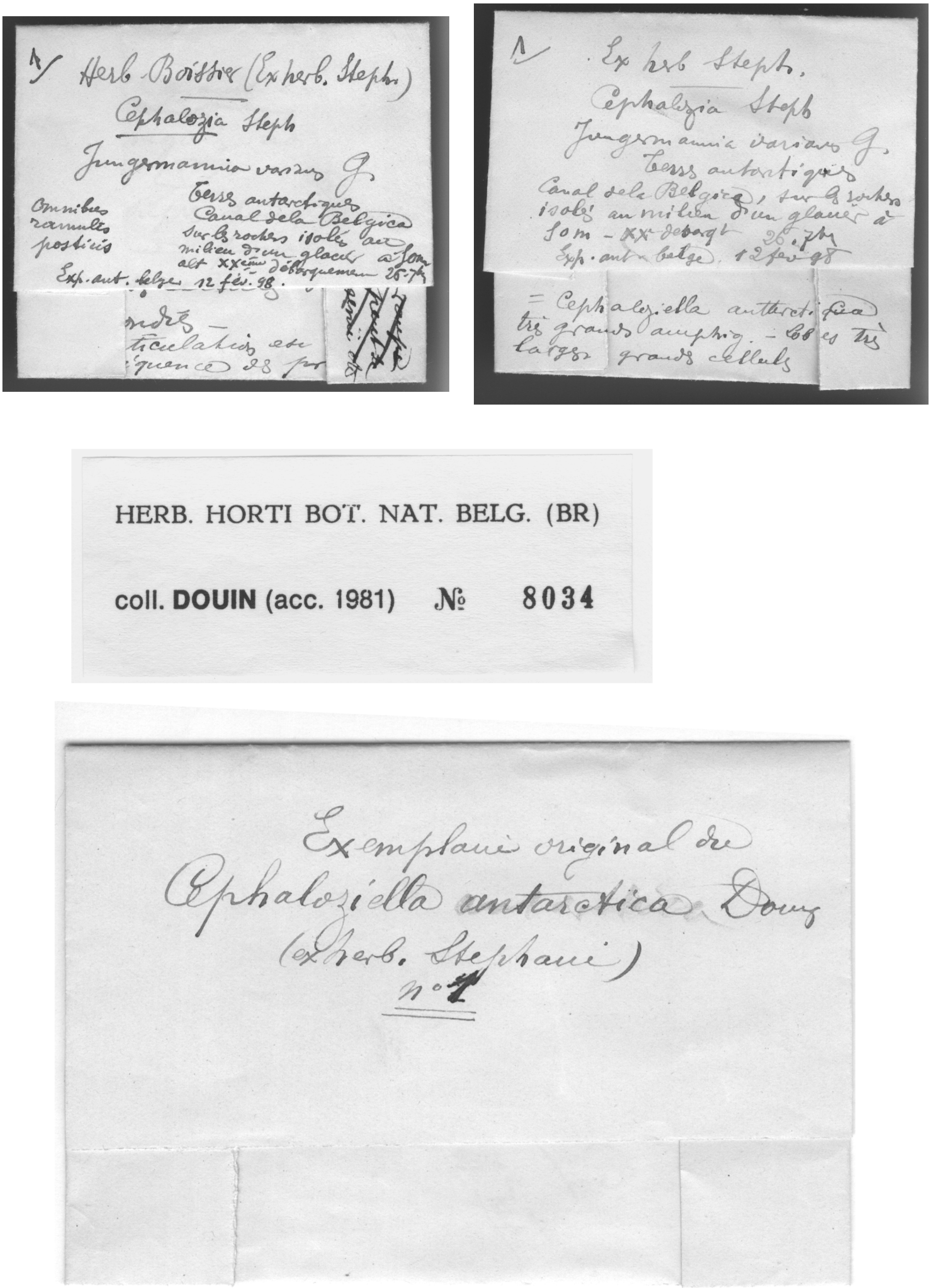
Stephani
det.

252g

FIGURE 10. Labels of the specimens of *Barbilophozia hatcheri* collected by E. Racovitza during the Belgian Antarctic Expedition (1897–1899) and deposited in BR.

Islands to the Fallières Coast on the south-western coast of the Antarctic Peninsula. These are available for investigation in the herbarium of this institute (AAS) and details of all specimens may be accessed on the Antarctic Plant Database (APD) (see Peat, 1998). All data concerning material held in AAS are available on the BAS Internet web site (http://www.nerc-bas.ac.uk/public/tflsd/aas.html or http://www.antarctica.ac.uk/Resources/BSD/PlantDatabase/aas_form.html).

Records of liverworts were published in general accounts on the Antarctic veg-



1/ Herb. Boissier (Ex herb. Steph.)

Cephalozia Steph.

Jungermannia varians G.

Omnibus ramulis posticis

Terres antarctiques
Canal de la Belgica
sur les rochers isolés au milieu d'un glacier à 50m alt XXème débarquement 25-7bre
Exp. ant. belge 12 fév. 98.

ndés —
ticulation est
équence de pr

1/ Ex herb Steph.

Cephalozia Steph

Jungermannia varians G.
Terres antarctiques
Canal de la Belgica, sur les rochers isolés au milieu d'un glacier à 50m - XXe debarqt 26.7bre
Exp. ant. belge 12 fev 98

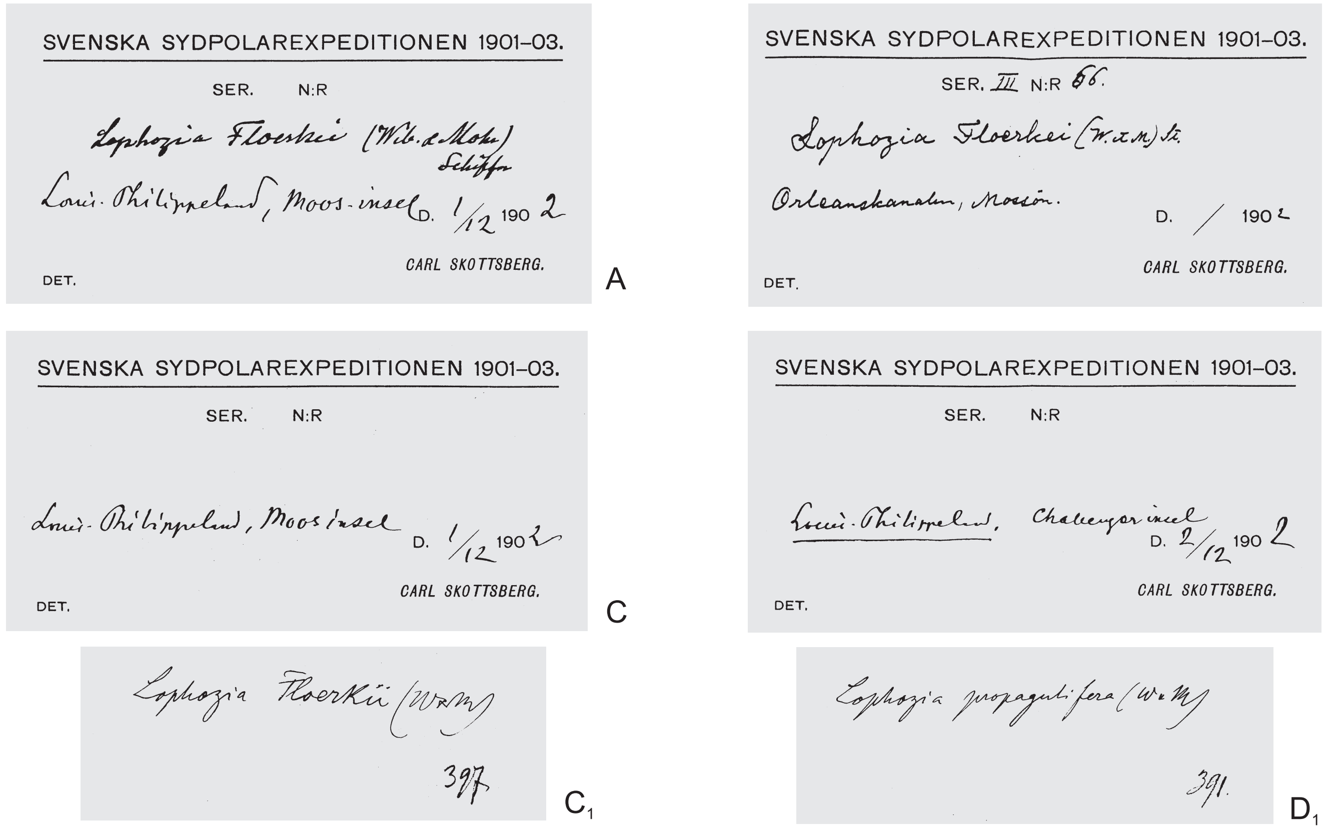
= Cephaloziella antarctica
très grands amphig. - Lobes très larges grands cellules

HERB. HORTI BOT. NAT. BELG. (BR)

coll. **DOUIN** (acc. 1981) № **8034**

Exemplaire original de
Cephaloziella antarctica Douin
(ex herb. Stephani)
n° 1

FIGURE 11. Details of the type material of *Cephaloziella antarctica* collected by E. Racovitza during the Belgian Antarctic Expedition (1897–1899) and deposited in BR.



SVENSKA SYDPOLAREXPEDITIONEN 1901–03.
SER. N:R
Lophozia Floerkei (Web. & Mohr) Schiffn
Louis-Philippeland, Moos-insel D. 1/12 1902
CARL SKOTTSBERG.
DET.

SVENSKA SYDPOLAREXPEDITIONEN 1901–03.
SER. III N:R 66.
Lophozia Floerkei (W. & M.) St.
Orleanskanalen, Mossön.
D. / 1902
CARL SKOTTSBERG.
DET.

SVENSKA SYDPOLAREXPEDITIONEN 1901–03.
SER. N:R
Louis-Philippeland, Moosinsel D. 1/12 1902
CARL SKOTTSBERG.
DET.

SVENSKA SYDPOLAREXPEDITIONEN 1901–03.
SER. N:R
Louis-Philippeland, Challengerinsel D. 2/12 1902
CARL SKOTTSBERG.
DET.

Lophozia Floerkii (W&M)
397

Lophozia propagulifera (W&M)
391.

FIGURE 12. Labels of the liverwort specimens collected by C. Skottsberg during the Swedish South Polar Expedition (1901–1903) and deposited in S. A–C – *Barbilophozia hatcheri* (C_1 – inside label); D – *Lophozia excisa* (D_1 – inside label).

etation (e.g. Greene, 1964*b*; Longton, 1966, 1967; Longton & Holdgate, 1967; Collins, 1969; Gimingham & Lewis Smith, 1970), but definitive determinations to species were mostly lacking. This was because the general state of the taxonomy of austral hepatics which was then in its infancy and no keys to determine species were available. For over 170 years of botanical exploration of Antarctica much confusion has existed regarding the exact status of many species which were uncritically reported in the literature. Steere (1965) drew attention to this: "The real problem ... is not to find in the published literature what names of what bryophytes have been reported, but to find out what these names mean".

Although eight hepatic species had been reported between 1960 and 1970 (Table 3), according to the present taxonomic concepts these represented only four species (Table 4). In addition, there were also some taxa still named only to genus, e.g. *Anthelia*, *Lepidozia* and *Metzgeria*.

R. M. Schuster in 1969 collected hepatics at 18 localities from King George Island in the South Shetland Islands south to Hook Island in the Biscoe Islands off the mid-western coast of the Antarctic Peninsula (Robinson, 1972). However, he provided only a brief report on his findings (Schuster, 1969*a*), and no detailed account of the species. Three species were reported as new to Antarctica and he implied the occurrence of three other species new to science. Of these, only one was later described, *Cephaloziella hispidissima* (Schuster, 1971), but from specimens from Tierra del Fuego and New Zealand, without citation of any Antarctic collections. Subsequently, Schuster informed us that his *C. hispidissima* was collected on Livingston Island, so we accept this 1969 record as the first report of this species from within the Antarctic, despite the paradoxical situation that at that time it was not yet validly published. Unfortunately, the status of the other two putative new species, *Cephaloziella autoica* and *Lophozia antarctica*, has never been clarified, whereas some other species, for example *Evansianthus georgiensis* and *Cephaloziella varians*, were only incidentally mentioned in other publications by this author (Schuster & Damsholt, 1974; Schuster, 1982). According to Schuster's (1969*a*) survey, the hepatic flora of the Antarctic Peninsula region consisted of 12 or possibly 13 species.

The first record of a liverwort in continental Antarctica was a collection of plants of the genus *Cephaloziella* made by G. A. Llano in 1962 near the U.S. Wilkes Station on Wilkes Land. The identity of continental populations of this genus has been a source of continual confusion, as noted by Steere (1965): "I have had the very stimulating experience of finding one hepatic among the collections that Dr. George A. Llano made at Wilkes Station, at the east end of the Antarctic Continent. The hepatic collected by Llano belongs to the highly complex and difficult genus *Cephaloziella* and has not yet been finally identified". Additional records of *Cephaloziella* from Victoria Land were given by Greene (1967).

During the 1970s there were several new hepatic records from the Antarctic, with the addition of 11 species to the flora (Table 4). These new records are mainly credited to Grolle (1971*b*, 1972*a*) who studied a major collection of hepatics made by R. E. Longton and M. W. Holdgate on the South Sandwich Islands in 1962 and 1964. The flora of this volcanic archipelago has many unique features, mostly because of the favourable habitats on heated ground around fumaroles which support at least six species of liverworts unknown or exceedingly rare elsewhere in Antarctica. Grolle also studied specimens from Signy and Elephant Islands, resulting in several new records, including *Roivainenia jacquinotii*, *Herzogobryum teres* and *Hygrolembidium isophyllum* which were referred to in the general accounts on the vegetation of these islands by Lewis Smith (1972) and Allison and Lewis Smith (1973). Grolle was also the first to provide the definitive name for Antarctic populations of *Anthelia* which belong to *A. juratzkana*.

An interesting record of *Marchantia polymorpha* from the volcanic Deception Island was provided by Young and Kläy (1971), and it is still the only record of this species from within the Antarctic botanical zone. However, since no specimen of this liverwort was available to us, there is some doubt about its correct identity. Lewis Smith (1984*b*, *c*) collected *M. berteroana* from the same site about 12 years later.

In the 1980s there were new advances in the study of Antarctic hepatics. The first chromosome counts were established for five species (Ochyra *et al.*, 1982), and three additional species were reported. Bell and Blom (1986) published the bryophyte flora of the isolated Bouvetøya in the Southern Atlantic and added *Herzogobryum atrocapillum* to the Antarctic liverwort flora. There were several new records for *Cephaloziella varians* in East Antarctica, including the Vestfold Hills (Seppelt, 1984, 1986) and Larsemann Hills, Princess Elizabeth Land (Seppelt, 1983*a*). The latter site is at lat. 69°30’S, long. 76°00’E and Seppelt (1983*b*) considered it to be the most southerly record for an hepatic. However, *C. varians* is locally frequent in Ablation Valley, Alexander Island (lat. 70°48’S, long. 68°21’W) in the southern province of the maritime Antarctic and, at that time, this was the farthest south record of an hepatic in the Southern Hemisphere (Lewis Smith, 1988*b*). Since then, this species has been reported from Cape Geology, Botany Bay, Southern Victoria Land (77°00’S), and this currently represents the farthest south record for a liverwort (Seppelt & Green, 1998).

The first detailed floristic, ecological and geographical account of the hepatic flora for an Antarctic region (King George Island, South Shetland Islands) was published by Ochyra and Váňa (1989*a*). It provided a key to determination of the species, maps of local distribution and relevant taxonomic discussion, as well as the first attempt to explain the taxonomic status of *Cephaloziella* in Antarctica. Moreover, *Hygrolembidium ventrosum* and *Scapania obcordata* were added to the Antarctic flora, the latter being the first record of the species in the Southern Hemisphere. Ochyra and Váňa (1989*b*) also summarized all literature records of Ant-

TABLE 3. Chronological synopsis of the liverwort species recorded in the Antarctic from 1901 to 2000. Names in boldface refer to currently accepted taxa; underlined names refer to currently accepted taxa and indicate their first Antarctic report under this name.

No.	Original determination	Current status	Publication
1.	*Lophozia hatcheri* (A. Evans) Steph.	***Barbilophozia hatcheri*** (A. Evans) Loeske	Stephani (1901: 4)
2.	*L. propagulifera* (Gottsche) Steph.	***Lophozia excisa*** (Dicks.) Dumort.	Stephani (1901: 4)
3.	*Cephalozia varians* (Gottsche) Steph.	***Cephaloziella varians*** (Gottsche) Steph.	Stephani (1901: 5)
4.	*C. cucullifolia* Steph.	***Cephalozia badia*** (Gottsche) Steph.	Stephani (1905: 2)
5.	*Lophozia badia* (Gottsche) Steph.	*C. badia* (Gottsche) Steph.	Stephani (1905: 8)
6.	*L. floerkei* auct. [*non* (F. Weber & D. Mohr) Schiffn.]	*Barbilophozia hatcheri* (A. Evans) Loeske	Stephani (1905: 8)
7.	*Cephaloziella antarctica* Douin	*Cephaloziella varians* (Gottsche) Steph.	Douin (1920: 78)
8.	*Orthocaulis floerkei* auct. [*non* (F. Weber & D. Mohr) H. Buch]	*Barbilophozia hatcheri* (A. Evans) Loeske	Steere (1961: 30)
9.	***Marchantia berteroana*** Lehm. & Lindenb.	*Marchantia berteroana* Lehm. & Lindenb.	Corte (1962: 5)
10.	***Pachyglossa dissitifolia*** Herzog & Grolle	*Pachyglossa dissitifolia* Herzog & Grolle	Schuster (1969*a*: 103)
11.	*Clasmatocolea georgiensis* (Gottsche) Grolle	***Evansianthus georgiensis*** (Gottsche) R. M. Schust. & J. J. Engel	Schuster (1969*a*: 103)
12.	***Cephaloziella hispidissima*** R. M. Schust.	*Cephaloziella hispidissima* R. M. Schust.	Schuster (1969*a*: 103)
13.	*C. autoica* R. M. Schust.	?	Schuster (1969*a*: 103)
14.	*Lophozia antarctica* R. M. Schust.	? ***Lophozia*** cf. ***groenlandica*** (Nees) Macoun	Schuster (1969*a*: 103)
15.	*Lophozia excisa* (Dicks.) Dumort.	*Lophozia excisa* (Dicks.) Dumort.	Schuster (1969*b*: 521)
16.	*Jamesoniella grandiflora* (Lindenb. & Gottsche) J. B. Jack & Steph.	***Cryptochila grandiflora*** (Lindenb. & Gottsche) Grolle	Gimingham & Lewis Smith (1970: 767)
17.	*Cephaloziella byssacea* of Schuster [*non* (Roth) Warnst.]	*Cephaloziella varians* (Gottsche) Steph.	Schuster (1971: 194)
18.	*Cryptochila grandiflora* (Lindenb. & Gottsche) Grolle	*Cryptochila grandiflora* (Lindenb. & Gottsche) Grolle	Grolle (1971*b*: 21)
19.	*Cephalozia badia* fo. *minor* Grolle	*Cephalozia badia* (Gottsche) Steph.	Grolle (1972*a*: 83)
20.	*Cephaloziella varians* fo. *minor* Grolle	*Cephaloziella varians* (Gottsche) Steph.	Grolle (1972*a*: 83)

21.	*Clasmatocolea koeppensis* (Gottsche) Grolle	***Clasmatocolea rigens*** (Hook. f. & Taylor) J. J. Engel	Grolle (1972*a*: 84)
22.	*Cryptochila grandiflora* fo. *tenuiretis* Grolle	*Cryptochila grandiflora* (Lindenb. & Gottsche) Grolle	Grolle (1972*a*: 84)
23.	*Lepidozia cuspidata* Steph.	***Lepidozia chordulifera*** Taylor	Grolle (1972*a*: 84)
24.	*Lophocolea secundifolia* Hook. f. & Taylor	***Lophocolea lenta*** (Hook. f. & Taylor) Gottsche, Lindenb. & Nees	Grolle (1972*a*: 84)
25.	***Riccardia georgiensis*** (Steph.) Hässel	*Riccardia georgiensis* (Steph.) Hässel	Grolle (1972*a*: 85)
26.	***Triandrophyllum subtrifidum*** (Hook. f. & Taylor) Fulford & Hatcher	*Triandrophyllum subtrifidum* (Hook. f. & Taylor) Fulford & Hatcher	Grolle (1972*a*: 85)
27.	***Herzogobryum teres*** (Carrington & Pearson) Grolle	*Herzogobryum teres* (Carrington & Pearson) Grolle	Lewis Smith (1972: 19)
28.	***Hygrolembidium isophyllum*** R. M. Schust.	*Hygrolembidium isophyllum* R. M. Schust.	Lewis Smith (1972: 19)
29.	***Marchantia polymorpha*** L.	*Marchantia polymorpha* L.	Young & Kläy (1971: 359)
30.	***Roivainenia jacquinotii*** (Mont.) Grolle	*Roivainenia jacquinotii* (Mont.) Grolle	Allison & Lewis Smith (1973: 187)
31.	***Anthelia juratzkana*** (Limpr.) Trevis.	*Anthelia juratzkana* (Limpr.) Trevis.	Allison & Lewis Smith (1973: 187)
32.	*Cephaloziella arctica* Bryhn & Douin	*Cephaloziella varians* (Gottsche) Steph.	Schuster & Damsholt (1974: 325)
33.	*C. exiliflora* auct. [*non* (Taylor) Douin]	*Cephaloziella varians* (Gottsche) Steph.	Fulford (1976: 417)
34.	*Lophocolea willii* Grolle	Erroneous report	Fulford (1976: 483)
35.	*Clasmatocolea rigens* (Hook. f. & Taylor) J. J. Engel	*Clasmatocolea rigens* (Hook. f. & Taylor) J. J. Engel	Engel (1980: 49)
36.	*Evansianthus georgiensis* (Gottsche) R. M. Schust. & J. J. Engel	*Evansianthus georgiensis* (Gottsche) R. M. Schust. & J. J. Engel	Schuster (1982: 17)
37.	***Herzogobryum atrocapillum*** (Hook. f. & Taylor) Grolle	*Herzogobryum atrocapillum* (Hook. f. & Taylor) Grolle	Bell & Blom (1986: 12)
38.	***Hygrolembidium ventrosum*** (Mitt.) Grolle	*Hygrolembidium ventrosum* (Mitt.) Grolle	Ochyra & Váňa (1989*a*: 193)
39.	***Scapania obcordata*** (Berggr.) S. W. Arnell	*Scapania obcordata* (Berggr.) S. W. Arnell	Ochyra & Váňa (1989*a*: 204)
40.	*Lepidozia chordulifera* Taylor	*Lepidozia chordulifera* Taylor	Ochyra & Váňa (1989*b*: 215)
41.	*Lophocolea lenta* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees	*Lophocolea lenta* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees	Ochyra & Váňa (1989*a*: 218)

TABLE 3. Continued.

No.	Recorded species	Current status	Publication
42.	*Gymnomitrion corallioides* auct. [*non* Nees]	*Herzogobryum teres* (Carrington & Pearson) Grolle	Chen *et al*. (1993: 50)
43.	*Marsupella boeckii* auct. [*non* (Austin) Kaal.]	*Lophozia excisa* (Dicks.) Dumort.	Chen *et al*. (1993: 50)
44.	*Cephalozia bicuspidata* auct. [*non* (L.) Dumort.]	*Pachyglossa dissitifolia* Herzog & Grolle	Chen *et al*. (1993: 50)
45.	*Odontoschisma macounii* auct. [*non* (Austin) Underw.]	*Herzogobryum teres* (Carrington & Pearson) Grolle	Chen *et al*. (1993: 50)
46.	***Metzgeria decipiens*** (C. Massal.) Schiffn.	*Metzgeria decipiens* (C. Massal.) Schiffn.	Lewis Smith (1996: 33)
47.	***Lophozia*** cf. ***groenlandica*** (Nees) Macoun	*Lophozia* cf. *groenlandica* (Nees) Macoun	Present work
48.	***Scapania gamundiae*** R. M. Schust.	*Scapania gamundiae* R. M. Schust.	Present work
49.	***Pachyglossa fissa*** (Mitt.) Herzog & Grolle	*Pachyglossa fissa* (Mitt.) Herzog & Grolle	Present work
50.	***P. spegazziniana*** (C. Massal.) Herzog & Grolle var. ***exilis*** Herzog & Grolle	*P. spegazziniana* (C. Massal.) Herzog & Grolle var. *exilis* Herzog & Grolle	Present work

TABLE 4. List of Antarctic liverworts arranged chronologically according to their first publish report.

No.	Species	Year of report	Author
1.	*Barbilophozia hatcheri* (A. Evans) Loeske	1901	F. Stephani
2.	*Lophozia excisa* (Dicks.) Dumort.	1901	F. Stephani
3.	*Cephaloziella varians* (Gottsche) Steph.	1901	F. Stephani
4.	*Cephalozia badia* (Gottsche) Steph.	1905	F. Stephani
5.	*Marchantia berteroana* Lehm. & Lindenb.	1962	A. Corte
6.	*Pachyglossa dissitifolia* Herzog & Grolle	1969	R. M. Schuster
7.	*Evansianthus georgiensis* (Gottsche) R. M. Schust. & J. J. Engel	1969	R. M. Schuster
8.	*Cephaloziella hispidissima* R. M. Schust.	1969	R. M. Schuster
9.	*Cryptochila grandiflora* (Lindenb. & Gottsche) Grolle	1971	R. Grolle
10.	*Clasmatocolea rigens* (Hook. f. & Taylor) J. J. Engel	1972	R. Grolle
11.	*Lepidozia chordulifera* Taylor	1972	R. Grolle
12.	*Riccardia georgiensis* (Steph.) Hässel	1972	R. Grolle
13.	*Lophocolea lenta* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees	1972	R. Grolle
14.	*Triandrophyllum subtrifidum* (Hook. f. & Taylor) Fulford & Hatcher	1972	R. Grolle
15.	*Herzogobryum teres* (Carrington & Pearson) Grolle	1972	R. I. Lewis Smith
16.	*Hygrolembidium isophyllum* R. M. Schust.	1972	R. I. Lewis Smith
17.	*Marchantia polymorpha* L.	1972	S. B. Young & J.-R. Kläy
18.	*Roivainenia jacquinotii* (Mont.) Grolle	1973	J. S. Allison & R. I. Lewis Smith
19.	*Anthelia juratzkana* (Limpr.) Trevis.	1973	J. S. Allison & R. I. Lewis Smith
20.	*Herzogobryum atrocapillum* (Hook. f. & Taylor) Grolle	1986	B. G. Bell & H. H. Blom
21.	*Hygrolembidium ventrosum* (Mitt.) Grolle	1989	R. Ochyra & J. Váňa
22.	*Scapania obcordata* (Berggr.) S. W. Arnell	1989	R. Ochyra & J. Váňa
23.	*Metzgeria decipiens* (C. Massal.) Schiffn.	1996	R. I. Lewis Smith
24.	*Lophozia* cf. *groenlandica* (Nees) Macoun	2000	H. Bednarek-Ochyra et. al.
25.	*Scapania gamundiae* R. M. Schust.	2000	H. Bednarek-Ochyra et. al.
26	*Pachyglossa fissa* (Mitt.) Herzog & Grolle	2000	H. Bednarek-Ochyra et. al.
27.	*P. spegazziniana* (C. Massal.) Herzog & Grolle var. *exilis* Herzog & Grolle	2000	H. Bednarek-Ochyra et. al.

arctic hepatics in a checklist, including some unpublished new regional records submitted by R. I. Lewis Smith, naming 22 species, with a further two still named only to genus. In addition, the phytogeography of Antarctic hepatics was outlined and nine distribution patterns were recognised.

In the 1990s new additions of hepatics to the Antarctic flora were published by Chen *et al.* (1993, 1995). They provided three unexpected records from King George Island, namely *Gymnomitrion corallioides*, *Marsupella boeckii* and *Odontoschisma macounii*, all recorded for the first time from the Southern Hemisphere, together with *Cephalozia bicuspidata*, also new to the Antarctic. However, all these records were based upon misidentifications and correctly referred to species reported earlier from this region. In the meantime, the Antarctic specimens consistently cited as *Metzgeria* sp. were finally named as *M. decipiens* (Lewis Smith, 1996).

The present work provides an additional four new regional species, namely *Lophozia* cf. *groenlandica*, *Scapania gamundiae*, *Pachyglossa fissa* and *P. spegazziniana* var. *exilis*. They are based upon specimens collected by scientists of the British Antarctic Survey from various localities in the Antarctic Peninsula region which had remained unnamed in AAS.

During a century of the hepaticological work, 50 taxa of liverworts have been reported from the Antarctic (Table 3). Of these, one report (*Lophocolea willii*) is erroneous, and another five taxon names are typical *nomina nuda*. Only two species new to science have been described from Antarctic material, namely *Cephalozia cucullifolia* and *Cephaloziella antarctica*. This markedly contrasts with mosses of which group 47 species and 14 infraspecific taxa were described as new to science, but only a very few have been accepted as good species (Ochyra *et al.*, 1998; Ochyra, 1998). After careful taxonomic revision of all available specimens, we conclude that the liverwort flora of the Antarctic currently comprises 27 species (Table 4).

Chapter 3

ECOLOGY AND CONSERVATION

THE ROLE OF LIVERWORTS IN ANTARCTIC PLANT COMMUNITIES

Throughout much of the maritime Antarctic liverworts are associated with mosses, but are seldom abundant over more than a few square metres. Within such stands very few species achieve dominance. With a few exceptions, liverworts do not develop distinct communities, but occasionally attain small-scale dominance within moss-dominated communities. The exceptions are some species associated with geothermal ground centred on active fumaroles on some of the South Sandwich Islands, and *Cephaloziella varians* and *Marchantia berteroana* both of which form small dense mats in suitable sites from the South Orkney Islands to Marguerite Bay in the south-west of the Antarctic Peninsula. An attempt to rationalise the cryptogamic communities into a subjective classification based on growth-form, dominance and constancy was developed by Gimingham and Lewis Smith (1970) and Lewis Smith (1972) for the Antarctic, and particularly Signy Island. The scheme was extended to some other regions of the maritime and continental Antarctic in which liverworts are present (e.g. Allison & Lewis Smith, 1973; Lewis Smith & Corner, 1973; Longton, 1973, 1979; Lewis Smith, 1988*a*).

Because of their dependence on moisture, liverworts are restricted to coastal sites, with few records above *ca* 300 m altitude. The occurrence of *Cephaloziella varians* on geothermal ground at the summit of Mt. Melbourne, Victoria Land (Fig. 2), at *ca* 2700 m altitude and *ca* 15 km inland is unique (Broady *et al.*, 1987). This species also occurs farther south than any other, reaching 77°00'S at Cape Geology, Botany Bay, south Victoria Land, East Antarctica (Seppelt & Green, 1998), and 70°52'S at Moutonnée Valley, Alexander Island, West Antarctica (Fig. 18) (Lewis Smith, 1988*b*). Although several species of moss are known from maritime and continental Antarctic lakes (Lewis Smith, 2000) there is only one record of a liverwort from an aquatic habitat. This exception is *Pachyglossa dissitifolia* which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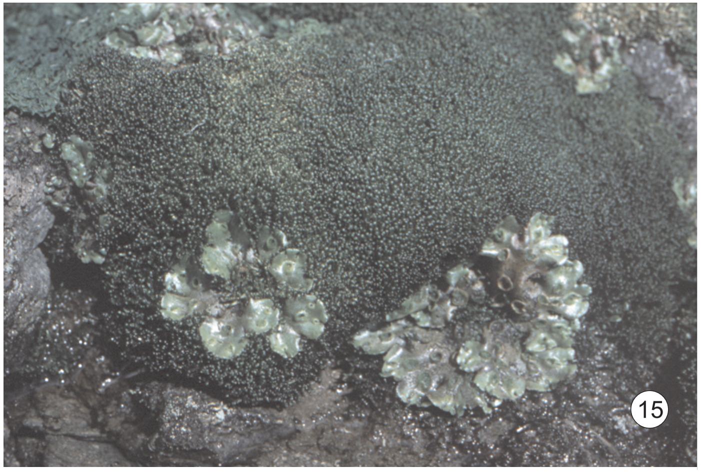
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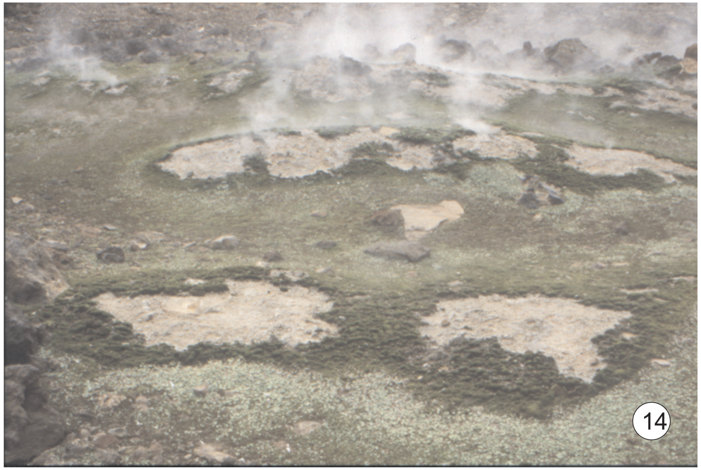
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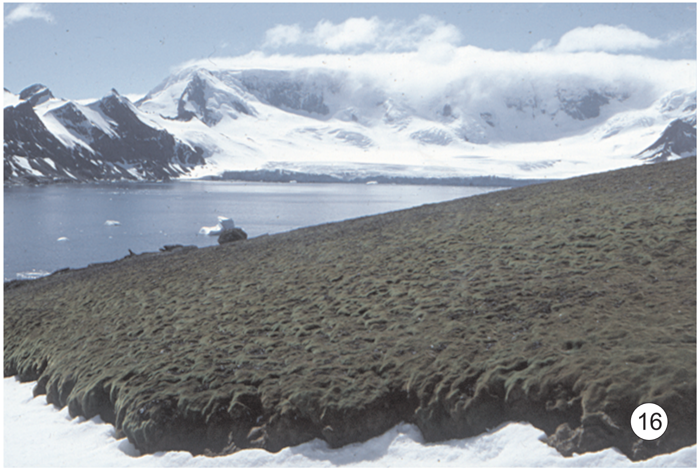
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was found amongst detached masses of *Warnstorfia sarmentosa* and *Drepanocladus longifolius* washed up along the shoreline of Midge Lake on Byers Peninsula, Livingston Island, South Shetland Islands. This moss and liverwort admixture grows at *ca* 1–2 m depth in the lake.

Unlike many mosses and lichens the occurrence of liverworts is restricted principally by the moisture regime of the substratum. Few, if any, appear to be influenced by the texture, chemistry or nutrient status of the soil, degree of shading, exposure to wind, or duration of winter snow cover. Some species have a wide ecological amplitude, occurring in various habitats, including shaded rock crevices (notably *Cephaloziella varians*, *Barbilophozia hatcheri* and *Pachyglossa dissitifolia*). The rare *Metzgeria decipiens* is restricted to shaded rock overhangs and amongst moss growing on moist shaded rock faces. *C. varians* is the most common and widespread of all liverworts in Antarctica (Figs 17–18). It is also of particular interest because of its rapid response to UV-B, changing from yellow-green to black within a few days of being exposed to high UV-B levels, and *vice versa* when screened from UV-B, by the production of a photoprotectant anthocyanin (Post & Vesk, 1992; K. K. Newsham, *pers. comm.*). Although several liverwort species occurring in the Antarctic have an association with a mycorrhizal fungi (e.g. *Lophozia*, *Scapania* and *Riccardia*), this has previously been reported only in *C. varians* (Williams *et al.*, 1994).

The three principal habitats occupied by liverworts are various fellfield communities, moss turf banks and geothermal areas. Antarctic fellfield varies from very sparsely vegetated, dry windswept mineral soil, gravel, stones and boulders to densely vegetated, moist habitats of similar nature but in relatively sheltered sites which retain late snow beds into summer. In the former category the terrain is often dissected by cryoturbic features such as stone and soil "streams" on gentle slopes, and networks of stone and soil polygons on level ground. On the stable margins of these, especially the solifluction features (Figs 18–20), several species of liverwort may be prominent (e.g. *Anthelia juratzkana*, *Cephalozia badia*, *Cephaloziella varians*, *Hygrolembidium isophyllum*, *Lophozia excisa*, *Pachyglossa dissitifolia*).

In the more sheltered moister sites, where mosses provide high cover, several

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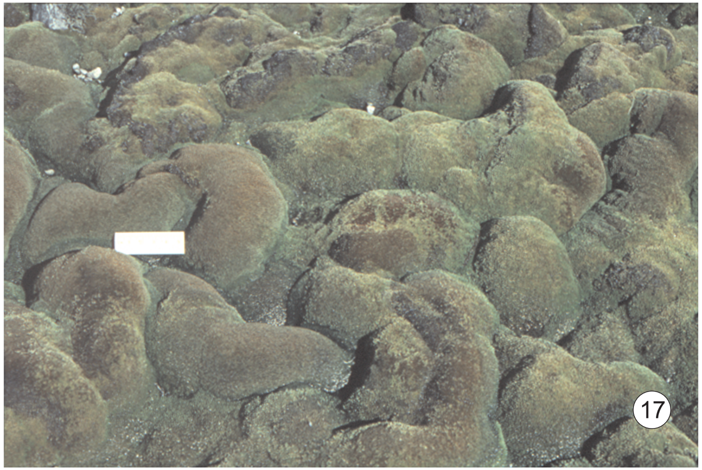
FIGURES 13–16. **13**. Hepatic-rich community around an active fumarole emitting steam on rim of crater at *ca* 100 m alt.; temperatures within *Cryptochila grandiflora* mats reach 40°. South Sandwich Is., Bellingshausen I., Basilisk Peak. **14**. Hepatic-rich community, dominated by *Marchantia berteroana*, on geothermal ground on inner slope of crater at *ca* 100 m alt.; the surface of the bare patches reach temperatures up to 65°C, while below the *Marchantia* thalli they reach *ca* 40°C. South Sandwich Is., Bellingshausen I., Basilisk Peak. **15**. *Marchantia berteroana* colonizing *Sanionia* sp. South Orkney Is., Signy I., North Point, *ca* 35 m alt. **16**. Extensive moss turf community formed by *Chorisodontium aciphyllum* and *Polytrichum strictum*, usually containing an abundance of *Barbilophozia hatcheri*, *Cephaloziella varians*, *Lophozia excisa* and very rarely *Lepidozia chordulifera*. South Orkney Is., Signy I., Moss Braes, *ca* 50–75 m alt. [Photos 13 and 14 by P. Convey; 15 and 16 by R. I. Lewis Smith.]



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liverwort species may be quite abundant (e.g. the above species, together with *Barbilophozia hatcheri* and *Herzogobryum teres*). Signy Island, South Orkney Islands, has a complex geology and is unique in having outcrops of limestone which produce highly alkaline soils (pH 7.5–9.0). While these possess a distinctive calcicolous moss and lichen flora, no liverworts are specific to these habitats, although *Marchantia berteroana* (Fig. 15) is most frequent on mildly alkaline soils (Lewis Smith, 1972).

The thick (often up to 1–2 m high) moss turf banks (Figs 5–6, 16) formed by *Chorisodontium aciphyllum* and *Polytrichum strictum* throughout the northern maritime Antarctic (Fenton & Lewis Smith, 1982; Fenton, 1980, 1982) harbour several species of liverwort, especially where the looser *Ch. aciphyllum* is dominant. The most frequently occurring of these are *Cephaloziella varians* and *Barbilophozia hatcheri*, but it is also the principal habitat of the rare *Lepidozia chordulifera*.

The liverwort-rich bryophyte communities associated with geothermal soil around fumaroles in the South Sandwich Islands (Figs 3, 13–14) are a unique feature in the Antarctic. These were first described by Longton (1966) and in more detail by Longton and Holdgate (1979) and Convey *et al.* (in press). These communities possess the greatest diversity of liverworts (11) anywhere in the Antarctic, several forming distinct concentric zones around the fumarole vents where the temperature of the soil 1–2 cm below the vegetation can reach 30–50°C. Several of the species occurring here are known nowhere else in the Antarctic or are extremely rare elsewhere (e.g. *Clasmatocolea rigens*, *Cryptochila grandiflora*, *Riccardia georgiensis*, *Triandrophyllum subtrifidum*). Liverworts are also associated with similar heated substrata on Deception Island, South Shetland Islands (e.g. *Marchantia polymorpha* and *M. berteroana*, see Young & Kläy, 1971; Lewis Smith, 1984*b*, *c*) and on the summit of Mt. Melbourne, Victoria Land (*Cephaloziella varians*, see Broady *et al.*, 1987).

CONSERVATION OF LIVERWORTS

Although very little is known about the liverworts of Antarctica, none is believed to be endangered. However, several species are described here as being rare,

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FIGURES 17–20. **17**. Convoluted turf of *Bryum pseudotriquetrum* (green) and *Ceratodon purpureus* (brown) with *Cephaloziella varians* (not visible) occurring in the moist depressions between the moss ridges. Wilkes Land, Windmill Is., Bailey Peninsula, *ca* 30 m alt. (the scale is 5 cm long). **18**. *Cephaloziella varians* in a bryophyte oasis at the southern limit of liverwort distribution in West Antarctica. Alexander I., Ablation Valley, ca. 10 m alt. **19**. *Anthelia juratzkana* (grey) and several mosses colonising the stable margin of a mobile stone stripe. South Orkney Is., Signy I., Moraine Valley, *ca* 30 m alt. **20**. *Herzogobryum teres* (grey) overgrowing *Cephaloziella varians*. South Orkney Is., Signy I., Moraine Valley, *ca* 35 m alt. [All photos by R. I. Lewis Smith.]

but this is mainly because very few collections have been made; they may well be much more frequent, but easily overlooked or mistaken for certain common species. Human impact is on such a small and localised scale that none of the 27 species is considered to be threatened. However, to a degree, all liverworts, indeed all plants and lichens, within the Antarctic Treaty Area are protected by the *Protocol on Environmental Protection to the Antarctic Treaty* (Anonymous, 1993), Annex II, Conservation of Antarctic Fauna and Flora (Article 3, Protection of Native Fauna and Flora). This states that no native plants (including fungi and lichens), or their propagules, may be removed or damaged in "such quantities that their local distribution or abundance would be significantly affected". Harmful interference is not permitted, i.e. by "significantly damaging concentrations of native terrestrial plants by landing aircraft, driving vehicles, or walking on them, or by other means" and "any activity that results in the significant adverse modification of habitats of any species or population of native .... plant .....". To achieve anything more than very small-scale collecting of samples or specimens requires the issue of a permit by the national agency to whom the collector is responsible.

There are many Antarctic Protected Areas (Sites of Special Scientific Interest and Specially Protected Areas; Bonner & Lewis Smith, 1985; Anonymous, 1997). Of these, several were designated because of the occurrence of extensive plant communities, some with a diverse flora, as one of their primary reasons for designation. Each has its own management plan (currently being revised) which strictly controls activities so as to afford maximum protection to the values for which the sites are being protected. One of these, Cryptogam Ridge (0.7 km^2) at *ca* 2700 m altitude on the summit of the volcano Mt. Melbourne in Victoria Land, is designated specifically because of the unique occurrence of a liverwort. The outline description for the site states "Designation on the grounds that the geothermal ground supports a unique community of bryophytes, algae, and microbiota, including the only known occurrence in the Antarctic of the moss *Campylopus pyriformis* and the very rare continental occurrence of the liverwort *Cephaloziella exiliflora* [=*C. varians*]." (Anonymous, 1997).

A unique situation exists at several localities in the northern maritime Antarctic where populations of Antarctic fur seals (*Arctocephalus gazella*) have been increasing rapidly since the mid-1970s. At Signy Island, for example, the annual summer influx of non-breeding male animals has increased from a few dozen in the early 1970s to over 20,000 from about 1990. Their impact on the lowland terrestrial ecosystem has been devastating and large expanses of bryophyte and lichen communities have been destroyed (Lewis Smith, 1988*c*, 1990*a*, 1997). Although many of these areas had relatively abundant liverworts, all of the island's species also occur beyond the reach of the seals.

Chapter 4

DIVERSITY AND PHYTOGEOGRAPHY

GENERAL FEATURES OF THE HEPATICOFLORA

The liverwort flora of Antarctica comprises only 27 species classified into 19 genera and 12 families. This small number is typical of the flora of far southern regions which are renowned for their low species diversity in all groups of plants (Bliss, 1979). For instance, the hepatic flora of Arctic Alaska comprises 135 species (Steere and Inoue, 1978), South Greenland – 135 species (Schuster, 1988), West Greenland – 136 species (Schuster & Damsholt, 1974) and Svalbard (at lat. *ca* 80°N) – 85 species (Frisvoll & Elvebakk, 1996).

In contrast, the corresponding phytogeographically subantarctic islands have much lower numbers of species: South Georgia – 67 (Hässel de Menendez, 1977, 1980*a*, including present additions of *Anthelia juratzkana* and *Herzogobryum teres*), Prince Edward Islands – 44 (Grolle, 1971*c*; Schuster, 1989, 1995*a*), Îles Crozet – 20 (Grolle, 1971*c*), Îles Kerguelen – 37 (Schiffner, 1906), Heard Island – 11 (Bergstrom & Selkirk, 1997), and Macquarie Island – 51 (Selkirk *et al.*, 1990). However, these numbers are considered to be underestimates because the subantarctic islands are still poorly investigated bryologically, and additions to the floras are expected with progress in field exploration, as well as in taxonomic revisions of individual genera and families.

There is a distinctly climate-related gradient in increasing liverwort diversity from the Antarctic (27 species), via South Georgia (67 species) and the Falkland Islands (131 species; Engel, 1990*a*) to the Brunswick Peninsula at the southernmost tip of mainland South America (193 species; Engel, 1978) and Southern Patagonia at lat. 51°–52°S (288 species; Hässel de Menendez *et al.*, 1984; Hässel de Menendez & Solari, 1985).

The relatively small number of liverwort species in the antipodal region is compensated by the evolutionary importance of taxa occurring there. The cool-temperate hepatic flora in the Southern Hemisphere is much richer than its Holarctic counterpart in taxonomically isolated, primitive and stenotypic taxa which are often regarded as living “fossils”. Schuster (1969*c*, 1972*a*, 1976, 1979*b*, 1981, 1982, 1984) has postulated that the evolution of the large and complex order Jungermanniales, which includes over 75% of all Hepaticae, probably originated in southern South America and New Zealand which represent dissected fragments of the supercontinent Gondwana.

The distribution of each species in the different geographical regions of the Antarctic is indicated in Table 5. Greatest diversity is in the climatically less severe South Orkney Islands (20 species) and South Shetland Islands (18 species), while most of those in the South Sandwich Islands (11 species) are associated with the microclimatically favourable geothermal areas. There is a marked increase in the severity of climatic conditions between the South Shetland Islands and northern Antarctic Peninsula, while the stormy Bransfield Strait creates a natural barrier to dispersal southwards. Several species, prominent in the South Shetland Islands do not appear to have crossed this oceanic boundary, for instance *Anthelia juratzkana*, or are very rare on the Antarctic Peninsula, for example *Cephalozia badia*, *Herzogobryum teres* and *Pachyglossa dissitifolia*.

Cephaloziella varians is the commonest hepatic, both in terms of abundance and distribution, being widespread throughout the maritime Antarctic to lat. 70°51’S on Alexander Island. Additionally, it is the only hepatic species known in continental Antarctica where it occurs at several widely scattered stations to lat. 77°00’S in Victoria Land, and on the eastern coast of the Antarctic Peninsula.

Several species have been recorded in at least five or six phytogeographical regions as presented in Table 5, namely *Lophozia excisa*, *Pachyglossa dissitifolia*, *Marchantia berteroana* and *Cephalozia badia*. Of these, the first two are common and often abundant, whereas the latter two are only locally frequent. Two other species, *Metzgeria decipiens* and *Lophozia* cf. *groenlandica*, are distributed at widely separated localities in three regions, but their populations are small and very infrequent.

Of the remaining 18 species ten occur in one region and eight in two regions. Some are locally frequent and abundant, for example *Anthelia juratzkana* on Signy and King George Islands, *Triandrophyllum subtrifidum* on heated ground around fumaroles on Candlemas Island and *Cryptochila grandiflora* on similar sites on Leskov, Candlemas and Bellingshausen Islands in the South Sandwich Islands and on Deception Island in the South Shetlands. Conversely, species such as *Scapania obcordata*, *S. gamundiae*, *Pachyglossa fissa* and *P. spegazziniana* var. *exilis* occur sparingly in very small populations, sometimes consisting only of few stems, concealed within moss turfs or mats and are easily overlooked because of the very small and inconspicuous size of the plants.

The richest liverwort flora in the Antarctic, comprising 20 species (including one undeterminable species of *Riccardia*), occurs on the small Signy Island in the South Orkney Islands. The island has a complex geology, ranging from acidic quartz-mica schist to basic amphibolite and limestone and, accordingly, has a much broader range of habitats available for plants than any other region in the Antarctic. Also, the island has been more intensively explored bryologically than any other, and this must have contributed to the high number of species recorded. It is likely that a similar number of species exist at suitable sites on Coronation Island (notably Cape Hansen).

King George Island in the South Shetland Islands has also been extensively studied bryologically (Ochyra, 1998), although only 11 species have been collected (Ochyra & Váňa, 1989*a*). A similar number of species should be expected on other islands in this archipelago which, however, have been less intensively investigated. For example, ten species have been discovered on Livingston Island, the second largest island in this archipelago, and seven species are known to occur on the volcanic Deception Island. These numbers clearly indicate a decrease with increasing latitude and climatic severity, although the main limiting factor appears to be differences in the range of habitat types. In the Antarctic Peninsula region the highest number of species (6) has been detected in the Argentine Islands area off the Graham Coast, while on Anvers Island, the largest island of the Palmer Archipelago, off the Danco Coast, five species have been recorded. On Alexander Island, in the southernmost part of the Antarctic Peninsula, only *Cephaloziella varians* is known.

Surprisingly, the volcanic South Sandwich Islands with many favourable ecological niches near the fumaroles have a relatively poor hepaticoflora. It consists of 11 species, four of which are known exclusively in this archipelago, and eight species have been recorded on each of Candlemas and Leskov Islands. However, some species grow here in great abundance, for example *Cryptochila grandiflora*, *Clasmatocolea rigens* and *Triandrophyllum subtrifidum*.

This distribution pattern of liverworts in the maritime Antarctic implies that particular species differ markedly in their tolerance of severe environmental conditions, and there are only a very few which have adapted physiologically to very low temperatures and long periods of continual daylight. This seems to confirm experimental studies of changing irradiance and UV-B levels on bryophytes, notably *Cephaloziella varians* (Post & Vesk, 1992; K. K. Newsham, *pers. comm.*).

Nearly two thirds of the total number of liverwort genera found in the Antarctic consists of single species. Only five genera, namely *Hygrolembidium*, *Cephaloziella*, *Lophozia*, *Scapania* and *Marchantia*, comprise two species each, and the largest genus (*Pachyglossa*) embraces only three species. Thus, the mean number of liver-

TABLE 5. Distribution of liverwort species in Antarctica.

Species	Bouvetøya	South Sandwich Islands	South Orkney Islands	South Shetland Islands	Nothern Antarctic Peninsula < 65°S	Southern Antarctic Peninsula >65°S	Continent	Status^a	Fertility^b	Geographic element^c
Triandrophyllum subtrifidum (Hook. f. & Taylor) Fulford & Hatcher		+						VR	S	T–PA
Hygrolembidium isophyllum R. M. Schust.			+	+				R	S	S–AM
H. ventrosum (Mitt.) Grolle			+	+				R	♀	T–AA
Lepidozia chordulifera Taylor		+	+					VR	S	T–SA
Cephalozia badia (Gottsche) Steph.		+	+	+	+	+		C	F	S–AM
Cephaloziella hispidissima R. M. Schust.			+	+				R	S	S–AP
C. varians (Gottsche) Steph.	+	+	+	+	+	+	+	C	F	BIP
Anthelia juratzkana (Limpr.) Trevis.			+	+				O	S	BIP
Barbilophozia hatcheri (A. Evans) Loeske			+	+	+	+		C	S	BIP
Cryptochila grandiflora (Lindenb. & Gottsche) Grolle		+		+				R	F	T–PA
Lophozia excisa (Dicks.) Dumort.		+	+	+	+	+		C	F	BIP
L. cf. *groenlandica* (Nees) Macoun			+		+	+		R	S	BIP
Roivainenia jacquinotii (Mont.) Grolle				+				VR	S	T–AM
Herzogobryum atrocapillum (Hook. f. & Taylor) Grolle	+		+					VR	S	S–PA
H. teres (Carrington & Pearson) Grolle	+		+	+		+		O	♀+♂	S–PA
Scapania gamundiae R. M. Schust.			+					VR	S	T–SA
S. obcordata (Berggr.) S. W. Arnell			+	+				VR	S	BIP
Clasmatocolea rigens (Hook. f. & Taylor) J. J. Engel		+						VR	♂	T–SA
Evansianthus georgiensis (Gottsche) R. M. Schust. & J. J. Engel				+				VR	?	S–AM

Lophocolea lenta (Hook. f. & Taylor) Gottsche, Lindenb. & Nees		+	+					VR	♀	T–AP
Pachyglossa dissitifolia Herzog & Grolle	+	+	+	+	+			O	S	S–AM
P. fissa (Mitt.) Herzog & Grolle			+					VR	S	S–AA
P. spegazziniana (C. Massal.) Herzog & Grolle var. *exilis* Herzog & Grolle				+				VR	♀	S–AA
Riccardia georgiensis (Steph.) Hässel		+	(+)	+				VR	♀+♂	T–AA
Metzgeria decipiens (C. Massal.) Schiffn. & Gottsche			+		+	+		O	S	T–PA
Marchantia berteroana Lehm. & Lindenb.		+	+	+	+	+		O	♀	T–PA
M. polymorpha L.				+				VR	S	C–PA
Total	4	11	20	18	8	8	1			

[a] Status: **VR** – very rare (1–2 localities); **R** – rare (3–5 localities); **O** – occasional (6–10 localities); **C** – common (11 and more localities).

[b] Fertility: **S** – sterile; **F** – with sporophytes; ♀ and ♂ – forming only female and male gametangia.

[c] Geographical elements: **T** – south-temperate: **T–SA**: American, **T–AP**: amphipacific, **T–AA**: amphiatlantic, **T–PA**: pan-temperate; **S** – subantarctic: **S–AA**: amphiatlantic, **S–AM**: American, **S–AP**: amphipacific, **S–PA**: circumsubantarctic; **BIP** – bipolar; **C–PA** – pan-continental.

wort species per genus in the Antarctic is 1.42. This ratio is typical for the polar regions of both Hemispheres, although it may be modified somewhat as a result of progress in the study of the underinvestigated areas.

Of twelve families of hepatics, nine comprise one or two species only. However, the Geocalycaceae are represented by six species belonging within four genera. The Lophoziaceae and Lepidoziaceae have, respectively, five and three species in four and two genera.

The majority of the liverworts (18 species) in the Antarctic have been found in the barren state (no information on the reproductive condition of *Evansianthus georgiensis* from Livingston Island is available). In four species (*Hygrolembidium ventrosum*, *Lophocolea lenta*, *Marchantia berteroana* and *Pachyglossa spegazziniana* var. *exilis*) female gametangia and perianths have been found, while in *Clasmatocolea rigens* male plants have been seen. In *Herzogobrym teres* plants with both male and female gametangia but no sporophytes have been observed. Sporophytes have been found in only four species, namely *Lophozia excisa*, *Cryptochila grandiflora*, *Cephalozia badia* and *Cephaloziella varians*, but even in these species they are very rarely produced. The discovery of sporophytes in the latter species has been critical for the proper determination of the taxonomic status of the Antarctic populations because the characters associated with the sex condition are of basic importance in this otherwise taxonomically difficult genus.

Many species of Antarctic liverworts abundantly produce gemmae which serve very effectively in asexual reproduction. In *Cephaloziella hispidissima* gemmae have not been previously described, but they have been found for the first time in plants collected on Signy Island.

PHYTOGEOGRAPHICAL ELEMENTS

The liverwort flora of Antarctica is composed of several floristic categories and many species show a clearly disjunct pattern in their global geographical distribution. Although several key areas in the cool-temperate zone of the Southern Hemisphere still require detailed investigation, knowledge of the disjunct distributions of austral hepatics is now generally quite good. Credit for this is due principally to R. M. Schuster, R. Grolle and J. J. Engel who have clarified many of the taxonomic questions enabling the global ranges of many taxa to be determined. Future investigations, especially field surveys of subantarctic islands, will certainly yield many additions and corrections to distributions of particular species, but it is unlikely that they will markedly alter the general distribution patterns currently accepted.

Few works present detailed regional phytogeographical analysis of the liverwort floras in austral regions. The Brunswick Peninsula of the southernmost mainland South America and the Falkland Islands were studied by Engel (1978, 1990*a*, respectively). Another important study was that of the Transecta Botanica de la Patagonia Austral between lat. 51° and 52°S; liverworts were collected along the east-west transect in Patagonia (Hässel de Menendez *et al.*, 1984; Hässel de Menendez & Solari, 1985). An outline of the phytogeographical elements in the liverwort flora of Antarctica was given by Ochyra and Váňa (1989*b*). In general, their scheme is still valid and needs only slight modifications as a result of new developments in taxonomy and phytogeography of antipodal liverworts.

All hepatic species occurring in Antarctica are classified into ten categories (Table 6). They represent four main elements, two of which are subsequently subdivided into four subelements.

TABLE 6. Conspectus of geographical elements of Antarctic liverworts.

Category	Number of species	Percentage of total flora
Subantarctic	**9**	**33.3**
Amphipacific	1	3.7
Amphiatlantic	2	7.4
Circumsubantarctic	2	7.4
American subantarctic	4	14.8
South-temperate	**11**	**40.7**
South American temperate	4	14.0
Amphipacific	1	3.7
Amphiatlantic	2	7.4
Pan-temperate	4	14.8
Bipolar	**6**	**22.3**
Pan-continental	**1**	**3.7**

Antarctic element

On the basis of their original identifications *Cephalozia cucullifolia* and *Cephaloziella antarctica* were considered to be endemic in the Antarctic. However, they are now considered to be conspecific with *Cephalozia badia* and *Cephaloziella varians*, respectively, which are known outside the Antarctic biome. Additionally, there have been a few infraspecific taxa proposed as new to science from Antarctic material (Grolle, 1972*a*), but these are no longer accepted as valid taxa. Schuster (1969*a*) suggested two putative new species, *Lophozia antarctica* and *Cephaloziella autoica*, but these taxa have never been described and so their status cannot be determined.

The only candidate amongst the currently accepted liverworts which could be first described from Antarctic material was *Cephaloziella hispidissima*. However, although it was referred to for the first time from Antarctica by Schuster (1969*a*), his description of this species was actually based on Fuegian and New Zealand specimens (Schuster, 1971). Thus, no endemic liverwort has so far been detected in the Antarctic and so, for the present, no Antarctic element appears to exist amongst the hepatics. Nonetheless, two species, *Scapania obcordata* and *Lophozia* cf. *groenlandica*, can be treated as 'false' endemics in this region. They are bipolar species but in the Southern Hemisphere they are so far known only from the Antarctic.

Subantarctic element

In the older phytogeographical literature this element is not usually recognised, and species belonging here have been variously merged with south-temperate species and considered jointly as a single category which has usually been termed as 'antipodal' (Schuster, 1963, 1969*c*, 1972*a*, 1976, 1979*b*, 1982, 1983*b*), 'subantarctic' (Grolle, 1969) or 'antarctic' (Fulford 1963*b*). However, a detailed analysis of the distribution patterns of species of both liverworts (Engel, 1978, 1990*a*; Ochyra & Váňa, 1989*b*) and mosses (Ochyra, 1998; Ochyra *et al.*, 1998) confirm the recognition of the subantarctic element as a separate entity. Species belonging within this element occur primarily on the subantarctic islands, from South Georgia in the west to Macquarie Island in the east. At more northerly stations in southern South America (including the Falkland Islands), on Tristan da Cunha and in South Africa they occur at high elevations where the environmental conditions are similar to those in the Subantarctic.

Nine species (33.3%) of the Antarctic liverwort flora belong to this phytogeographical element. However, it is heterogeneous and comprises four distinct subelements.

Amphipacific Subantarctic subelement — This category comprises species occurring on subantarctic islands in the Australasian and South American sectors and occasionally penetrating northwards at high altitudes. A single species, *Cephaloziella hispidissima*, is placed in this subelement (Fig. 36). Formerly, Ochyra and Váňa (1989*b*) considered this species to be amphipacific south-temperate, but because the only known locality in New Zealand is in the alpine zone on South Island (Schuster, 1996*a*), the phytogeographical status of *C. hispidissima* was changed. Additionally, this species has most stations in the maritime Antarctic, and in southern South America it is still known only from the type locality in Tierra del Fuego at high elevations at Paso Garibaldi.

Amphiatlantic Subantarctic subelement — Species occurring within the South American, Atlantic and occasionally South Indian Ocean sectors of the Subantarctic constitute this category. It is represented by two species (7.4% of the flora) of the otherwise subantarctic genus *Pachyglossa*, namely *P. fissa* (Fig. 81) and *P. spegazziniana* var. *exilis* (Fig. 83).

Circumsubantarctic subelement — The species of this subelement occur on all or most subantarctic islands, and occasionally extend to New Zealand and mainland South America but only at high altitudes. In the Antarctic hepaticoflora it is represented by only two species (7.4% of the flora) of the antipodal genus *Herzogobryum*, *H. atrocapillum* (Fig. 61) and *H. teres* (Fig. 63).

American Subantarctic subelement — This subelement has four species (14.8% of the flora) which are restricted in their distribution to South Georgia and extend southwards to the northern maritime Antarctic, but are rare in the alpine belt in the *Nothofagus* zone in Patagonia. They are *Cephalozia badia* (Fig. 33), *Evansianthus georgiensis* (Fig. 73), *Hygrolembidium isophyllum* (Fig. 24) and *Pachyglossa dissitifolia* (Fig. 78).

South-Temperate element

This element comprises species which are restricted in distribution to the cool south-temperate zone. They are widespread in the Australasian and South American parts of the austral region, and some extend into southern Africa and Tristan da Cunha. Moreover, some south-temperate species extend into the tropics, especially along the Andean cordillera. This is a broad phytogeographical category which may be subsequently subdivided into further subelements according to distribution patterns of species south of the equator. This element contains the majority of the Antarctic hepaticoflora (11 species, 40.7% of the total flora).

South American Temperate subelement — This subelement consists of species having the main centre of occurrence in southern South America, including the Falkland Islands and South Georgia and extending to the northern maritime Antarctic. They also penetrate northward to the Valdivian region and occasionally to the northern Andes, but mainly in alpine areas. Four species (14.8% of the total flora) occur in the Antarctic: *Lepidozia chordulifera* (Fig. 30), *Roivainenia jacquinotii* (Fig. 59), *Scapania gamundiae* (Fig. 66) and *Clasmatocolea rigens* (Fig. 71).

Amphipacific subelement — This distribution pattern comprises taxa which share broadly the range of southern beeches, and hence it is sometimes called the *Nothofagus* type (Seki, 1974). A single species (3.7% of the flora), *Lophocolea lenta*, is distributed in temperate regions of southern South America, and disjunct in the Australasian sector (Fig. 75).

Amphiatlantic subelement — This subelement comprises two species (7.4% of the flora), *Hygrolembidium ventrosum* (Fig. 27) and *Riccardia georgiensis* (Fig. 86) which are distributed mainly in the temperate regions of southern South America and extend to the subantarctic islands in the Indian Ocean sector or to Tristan da Cunha/Gough group in the South Atlantic. They are not considered as subantarctic species because their northward extensions from the subantarctic are not restricted to higher elevations.

Pan-Temperate subelement — Species of this subelement are generally widespread and locally abundant throughout all the temperate regions of the Southern Hemisphere. They occur in southern South America and disjunct in New Zealand, south-eastern Australia, Tasmania, southern Africa and on the islands in the subantarctic and cool temperate zone, but frequently they penetrate into the tropics where they occur in the alpine zone. Four Antarctic species (14.8%) belong within this category, namely *Cryptochila grandiflora* (Fig. 49), *Marchantia berteroana* (Fig. 92), *Metzgeria decipiens* (Fig. 89) and *Triandrophyllum subtrifidum* (Fig. 22).

Bipolar element

This element includes the most widespread and common species of Antarctic liverworts which are also widely distributed in the Northern Hemisphere and disjunct in Australasia and/or in southern South America or Antarctica. Some have transitional localities at higher elevations in tropical and equatorial areas. The bipolar distribution pattern of mosses has been discussed by Schuster (1969*c*, 1983*b*), Schofield and Crum (1972), Schofield (1974), Ochyra (1992) and Ochyra and Lewis Smith (1996). Among the Antarctic liverworts this category consists of only six species (22.3%): *Anthelia juratzkana* (Fig. 43), *Barbilophozia hatcheri* (Fig. 46), *Cephaloziella varians* (Fig. 39), *Lophozia excisa* (Fig. 53), *L.* cf. *groenlandica* (Fig. 56) and *Scapania obcordata* (Fig. 68). These species are not particularly primitive and it is likely that they reached their present southern ranges via long-distance dispersal along the mountain ranges and land-bridges rather than as a result of break-up of ancient continuous ranges.

Pan-continental element

Only one species (3.7% of the total flora), *Marchantia polymorpha* (Fig. 95), has a subcosmopolitan range. This is a very widespread and “weedy” species growing on disturbed and open sites. It was found in such a habitat on the volcanic Deception Island immediately after the 1969 eruption (Young & Kläy, 1971) and it has not been rediscovered since. We could not acquire the voucher specimens for examination, so it is possible that the species could have been mistaken for the morphologically similar species *M. berteroana* which does occur sporadically on the island, including the *M. polymorpha* site (Lewis Smith, 1984*b*, *c*, 1988*d*).

ORIGIN OF THE LIVERWORT FLORA

A feature of the liverwort flora of Antarctica is the high proportion of the antipodal taxa in the broad sense, represented here by two phytogeographical elements, subantarctic and south-temperate species. They constitute *ca* 75% of the total number of species. This is in sharp contrast with the moss flora in which the antipodal element comprises less than half the species. Bipolar and pan-continental species comprise a fairly small number of liverwort species which make up only *ca* 25% of the total flora, whereas in the moss flora these two elements contribute more than half the species. However, despite the lower percentage, bipolar species are dominant liverworts in the Antarctic, whereas most of the antipodal taxa appear to be rare and sparse.

The lack of endemic taxa and dominance of bipolar species suggest that the liverwort flora of Antarctica is relatively young, a conclusion that is supported by the tectonic history of the continent. Antarctica, including offshore archipelagoes, was completely covered by continental glaciations from from Oligocene (*ca* 60 m. y. ago) until the Pleistocene (1 m. y. ago). There is palaeobotanical evidence that during the Oligocene forest existed in Antarctica and, probably until the Miocene (23–12 m. y. ago), relatively complex alpine communities must have persisted around the moister coastal fringes of the continent.

Little is known about the liverwort flora of Antarctica from before the Tertiary. As elsewhere, fossil liverworts are comparatively rare in the Southern Hemisphere. However, during the Lower Cretaceous (*ca* 140–130 m. y. ago) hepatics formed an important component of the flora of Alexander Island (Cantrill, 1997). Thalloid taxa belonging to the order Marchantiales predominated. *Marchantites rosulatus* Cantrill, *Thallites bicostatus* Cantrill and *Thallites* sp. formed distinct carpets on freshly deposited river sands and muds. Within establishing plant communities *Marchantites pinnatus* Cantrill and *M. taenioides* Cantrill formed a ground layer beneath fern thickets. Swamp communities with conifers contained *M. undulatus* Cantrill, *Hepaticites minutus* Cantrill and *Hepaticites* spp. The high diversity and relative abundance of individual liverwort taxa appeared to be a special feature of high latitude vegetation during the Cretaceous.

Another Lower Cretaceous liverwort flora has been reported from President Head, Snow Island, south-west of Livingston Island in the South Shetland Islands (Cantrill, 2000). The palaeontological interpretation suggests that these plants existed in a freshwater lake or adjoining swamp and that they had a strong affinity with the Gondwanan floras of both South America and Australia. The taxa included the leafy liverwort *Jungermannites stonei* Cantrill and three thalloid species, two belonging to *Hepaticites* and *Thallites* sp. Another jungermannialean liverwort, *Schizolepidella gracilis* Halle, from the Late Jurassic-Early Cretaceous, is known from Mt. Flora, Hope Bay, northern Trinity Peninsula (Gee, 1989); however, this material is now considered to belong to the Early Jurassic (200–180 m. y. ago; D. J. Cantrill, *pers. comm.*).

These few data strongly support the hypothesis promoted by Schuster (1969*c*, 1972*a*, 1976, 1979*b*, 1981, 1982, 1983*b*) that a specialized flora of *Glossopteris* and associated plants which had occurred in the Southern Hemisphere in the late Palaeozoic and subsequent araucarian floras of the Mezozoic, were rich in liverworts. Descendants of these ancient Hepaticae persit in the present subantarctic flora in various groups of liverworts.

It seems unlikely that hepatic taxa have survived an ecological catastrophe *in situ* on nunataks, during the glacial epochs when water, a critical requirement for hepatics, would have been virtually unavailable. Thus, most, if not all, of the present liverwort flora must be post-Pleistocene immigrants.

The nearest likely source of immigrant species that recolonised the Antarctic continent is South America, some 700–1000 km distant. It could not have been South Georgia because this island was covered by its own ice sheet extending 60 km offshore (Sudgen & Clapperton, 1977). The chance of bird dispersal is very slight because there are no land birds in the Antarctic and sea birds come ashore only to breed. However, skuas, gulls, terns and sheathbills migrate to southern South America but rarely visit inland sites. They probabaly do occasionally settle on bog or marsh habitats near the coast and could pick up vegetative propagules or spores of hepatics on their feet or feathers.

A more probable hypothesis is that wind is the most likely dispersal agent. The nature and effectiveness of long-distance dispersal is a crucial biogeographic problem. Data on the potential longevity of dormant propagules of hepatics are scanty. Vegetative shoots of *Cephaloziella varians* from the Antarctic have been found to be capable of growth after having been frozen for periods of from three years (Longton & Holdgate, 1967) to 20 years (Lewis Smith, unpublished data). Also, some experimental studies on the trans-oceanic dispersal of moss spores in the Southern Hemisphere implied its great importance in the establishment of the present day ranges (Zanten, 1976, 1978). This may also be valid for most species of liverworts occurring in the Antarctic. Several produce abundant vegetative structures capable of developing new plants. It would not be impossible for these to be carried long distances during storm events and, if deposited in favourable habitats in the Antarctic, may be capable of becoming established.

Chapter 5

SYSTEMATIC TREATMENT

AIMS AND OBJECTIVES

Ochyra and Váňa (1989*a*) provided descriptive, ecological and distributional accounts of the liverwort flora of King George Island, as well as an overview of liverwort distribution throughout the Antarctic (Ochyra & Váňa, 1989*b*). Chen *et al.* (1995) published similar accounts (in Chinese) for the liverwort flora of Fildes Peninsula (King George Island). The only continental Antarctic hepatic, *Cephaloziella varians*, has been described and illustrated by Kanda (1987, in Japanese), Seppelt (1983*a*, 1984, 1986) and Seppelt and Green (1998).

Amongst the Antarctic terrestrial plant groups knowledge of the composition of the liverwort flora remained obscure and inadequate until recently, and the taxonomic status of many taxa was very imprecise. This is a major problem for any ecological studies which rely on accurate identification of floristic components of communities or ecosystems. Similarly, the identity of some of the commonest species was suspect, while for others it was virtually impossible to separate one taxon from another in the field, for example species of *Cephaloziella*, *Cephalozia, Lophozia* and *Pachyglossa*. Clearly, any ecological, biogeographic or comparative studies can be valid only if the identity of the plants is accurately known. With increasing research on terrestrial ecosystems and their biota in Antarctica, particularly with regard to physiological tolerances and responses to changing climate, there is an urgent need for the liverwort (as well as the moss and lichen) flora to be revised.

At the start of this work a total of 26 species of liverworts had been reported in the literature from within Antarctica (Ochyra & Váňa, 1989*b*; Chen *et al.*, 1995). Several accounts proved to be uncritical and examination of voucher collections, if available, revealed they had been based upon misidentification. On the other hand, the present investigations showed the occurrence in Antarctica of several interesting and rare species which have not been hitherto reported from this biome, and one species is recorded for the first time in the Southern Hemisphere. To a large extent the new records balanced the taxa exluded from the flora, as a result of the present critical studies, so the final number of the species has remained largely unchanged (27).

The primary aim of this treatment is to provide descriptions and illustrations of all species of hepatics now known to occur in the Antarctic, as well as keys for their identification. In addition, the distribution of all species is discussed and, to illustrate the phytogeographical affiliation of the Antarctic hepaticoflora, the global distribution of each species is also mapped.

During the course of the preparation of this Flora all available historical collections made by early Antarctic expeditions and deposited in major world herbaria were revised. Examination of type collections of species described from Antarctica was of particular importance since it made it possible to establish their true identity. In some cases sub-Antarctic and southern South American taxa have been consulted, including types, because some taxonomic problems could be satisfactorily resolved only after examination of the taxa in question in the broadest geographical scope. In accordance with normal practice in this type of taxonomic work, as far as possible the relevant type collections of species have been located and studied.

Apart from historical collections a large number of recent collections have been examined. The richest collection of hepatics from Antarctica is deposited in the herbarium of the British Antarctic Survey in Cambridge, UK (AAS) and it is the basis of the present treatment. It was made predominantly by R. I. Lewis Smith and other scientific staff of this institute mainly since the early 1960s in a wide range of habitats and localities, mostly throughout the maritime Antarctic, from the South Sandwich Islands to Alexander Island. It yielded a particularly large number of new bryogeographical records as well as taxa new to this region.

Another valuable collection of Antarctic liverworts was made by R. Ochyra (1979–1980) on King George Island, the largest island in the South Shetland Islands archipelago. The latter collection was the basis for the study of local distributions and ecology if the island's liverworts (Ochyra & Váňa, 1989*a*). Some specimens from this area have been distributed in the *Bryophyta Antarctica Exsiccata* (Ochyra, 1984; Ochyra *et al.*, 1986) and these are the first Antarctic specimens of liverworts widely available for investigations.

In practice, most voucher collections of hepatics cited in the Antarctic botanical literature have been studied. Unfortunately, we had no access to the important collection made by R. M. Schuster in 1969 on the western coast of the Antarctic Peninsula and in the South Shetland Islands. This allegedly included *Evansianthus georgiensis*, the only record of this species from Antarctica (Schuster, 1969*a*, 1982).

All specimens studied for this Flora are listed in the entry "Specimens examined" and, separately, all literature records are also provided.

ARRANGEMENT OF THE FLORA

The Flora provides descriptions and illustrations, as well as phytogeographical and ecological information, for 27 species belonging within 19 genera and 12 families. It is a specimen-based Flora and, wherever possible, type specimens have been examined. Type information is given for all species and, according to normal practice, the type is cited from the published protologue, followed by data taken from the herbarium labels. For each species name all homotypic synonyms are given and, additionally, some heterotypic synonyms are provided if they are used for taxa described or reported from material collected in Antarctica. Moreover, for all taxa described from Antarctica and many species described from the subantarctic islands, the names are typified and, for some, new lectotypes are selected. Examination of type material is indicated within the text by the citation of an *Index Herbariorum, Ed. 8* acronym (Holmgren *et al.*, 1990) at the end of the type information.

The families are treated sequentially in approximately the same phylogenetic system as outlined by Schuster (1979*a*, 1984) and Grolle (1983*a*). To facilitate ease of reference, the genera are arranged alphabetically within the families, and species in alphabetic order within genera. Descriptions of families, genera and species are rather short and emphasize only features critical for recognition. Because most populations of Antarctic hepatics are sterile, the generic keys refer to species found in Antarctica, but generic descriptions refer to the genera as a whole, not just to the local species.

For each species short, concise ecological notes based on our field experience or taken from specimen labels follow the description. The distribution of all species is based on the examination of specimens, although in a few cases some literature reports are also marked on maps if they constitute phytogeographically important records, but are marked by a different symbol. All species reported from Antarctica on the basis of misdetermined specimens are placed in a “Species excluded” section. If necessary, the taxonomic status of the Antarctic material is discussed in greater detail, and for each species brief taxonomic and nomenclatural notes are also provided.

Two distribution maps are usually presented for each species. One illustrates the detailed distribution in Antarctica and the second provides its global range. The distribution of a species within each area is documented by the citation of all specimens examined. An indication of the world distribution of each species, based on an examination of specimens or extracted from reliable literature reports, is given.

The illustrations include in most cases habit, leaves and various cellular details which are taxonomically important. In fertile species details of perianths and sporophytes are also presented.

KEY TO GENERA OF ANTARCTIC LIVERWORTS

The following key comprises 19 genera which have been identified from Antarctica. Eleven are widely distributed throughout the world or at least in the Northern Hemisphere. They are mostly well defined and distinct, and their recognition should not pose difficulties for those who are not familiar with antipodal hepatics. The remaining eight genera are exclusively confined to the austral regions but many penetrate northwards into the tropics. These are not commonly known to bryologists, although they are also distinct, well-defined and easily recognised taxa.

The key to the Antarctic genera is partly artificial and refers rather to species of the region. This is because the generic characters in hepatics are usually assigned to sporophytes, and few Antarctic species produce mature sporophytes; even then they are very rare. Therefore, it would be highly impractical and unwise to use them in the key. Consequently, gametophyte characters are emphasised and used which should enable a quick and reliable identification of the material. For the same reason we declined from constructing a familial key because families in the Hepaticae are also mostly diagnosed by sporophyte criteria (Schuster, 1984).

It is probable that, with progress in field investigations and more detailed examination of existing collections, further species and genera of liverworts will be detected in Antarctica. Certainly, they may be recruited from taxa occurring in the *Nothofagus* zone of southern South America, and the finding of *Scapania gamundiae* at its second locality in Antarctica seems to confirm this assumption.

The basic reference work for the liverworts of the Patagonian region is still Schuster's (1963) treatment, although it is now rather out-of-date as considerable progress in taxonomic research on antipodal hepatics has since been achieved. As a result, many large and heterogeneous genera have been split into smaller but better-defined genera. The same is also true for the generic key in the first part of *Manual of the leafy Hepaticae of Latin America* (Fulford, 1963*a*). The most relevant works comprising keys to genera from the South American biome are two floras by Engel (1978, 1990*a*) dealing with the hepatics of the Magellanian region and the Falkland Islands. Just prior to submitting the present work Schuster (2000) published the first part of his *Austral Hepaticae* which, when completed, will be the most comprehensive treatment of the liverworts in the Southern Hemisphere.

KEY TO THE ANTARCTIC GENERA OF MARCHANTIOPSIDA

1. Plants thallose 2
1. Plants foliose 4

    2. Thallus with air chambers and pores . . . . ***Marchantia***
    2. Thallus without air chambers and pores 3

3. Thallus with a midrib . . . . ***Metzgeria***
3. Thallus without a midrib . . . . ***Riccardia***

4. Underleaves absent and if sometimes present then small, filamentous or subulate and mostly on the top of stems 5
4. Underleaves present 10

5. Leaves unlobed 6
5. Leaves bilobed 7

6. Plants small, julaceous, in compact tufts or mats; leaves bordered with 1–4 rows of hyaline cells; underleaves always absent . . . . . ***Herzogobryum***
6. Plants larger, not julaceous and growing in loose tufts; leaves not bordered by hyaline cells; small underleaves sometimes present . . . . . ***Cryptochila***

7. Leaves conduplicate, keeled; leaf lobes of different size . . . . . ***Scapania***
7. Leaves never conduplicate and keeled; leaf lobes more or less of the same size 8

8. Plants small, julaceous; leaves transversely inserted; leaf margin bordered by hyaline cells . . . . . ***Herzogobryum***
8. Plants not julaceous; leaves more or less obliquely inaserted, never bordered by hyaline cells 9

9. Gemmae present; leaf cells thin-walled, sometimes with small trigones . . . . . ***Lophozia***
9. Gemmae absent; leaf cells with slightly thickened walls, constantly without trigones . . . . . ***Cephalozia***

10. Leaves unlobed 11
10. Leaves 2–4-lobed 15

11. Plants ± isophyllous; underleaves only slightly smaller than leaves 12
11. Plants distinctly anisophyllous; underleaves much smaller than leaves 13

12. Leaves contiguous; plants julaceus; leaves widely cordate; leaf lamina unistratose . . . . . ***Hygrolembidium***
12. Leaves remote; plants never julaceous; leaves ovate; leaf lamina (at least at base) 2-polystratose . . . . . ***Pachyglossa***

13. Leaves ± 2-multistratose, at least at base; underleaves widely ovate to ovate triangular, always present 14
13. Leaves unistratose; underleaves filamentous to subulate, sometimes absent . . . . . ***Cryptochila***

14. *Anomoclada*-type of branching present; leaves reniform; leaf margin entire; underleaves sometimes slightly bilobed at the top . . . . . ***Evansianthus***
14. *Anomoclada*-type of branching absent; leaves widely cordate to irregularly ovate; leaf margin shallowly repand; underleaves crenate at the top . . . . . ***Hygrolembidium***

15. Leaves 3–4-lobed 16
15. Leaves 2(–3)-lobed 18

16. Plants ± suberect, leaf insertion ± transverse; leaves and underleaves (2–)3-lobed . . . . . ***Triandrophyllum***
16. Plants prostrate, leaf insertion oblique; leaves (3–)4-lobed 17

17. Underleaves 3–4-lobed with non-ciliate margin, similar to lateral leaves . . . . . ***Lepidozia***
17. Underleaves bilobed with ciliate margins, different in shape from lateral leaves . . . . . ***Barbilophozia***

18. Plants ± isophyllous, mostly suberect 19
18. Plants clearly anisophyllous, prostrate 20

19. Leaves and underleaves slightly bilobed to retuse; leaf lamina multistratose; plants lacking whitish colour . . . . . ***Pachyglossa***

19. Leaves and underleaves deeply bilobed; leaf lamina unistratose; plants when dry mostly whitish . . . . ***Anthelia***

    20. Plants very small, filiform; leaves mostly only twice or less wider than the stem . . . . ***Cephaloziella***
    20. Plants larger, not filiform; leaves mostly more than twice wider than the stem 21

21. Cuticle of the leaf cells coarsely verrucose; underleaves setaceous-ciliate . . . ***Roivainenia***
21. Cuticle of the leaf cells never coarsely verrucose; underleaves bilobed 22

    22. Leaves concave, widely ovate; underleaves bilobed, mostly without lateral teeth, only slightly wider than the stem . . . . ***Clasmatocolea***
    22. Leaves plane, narrowly ovate; underleaves bilobed with 1–2 lateral teeth, mostly twice wider than the stem . . . . ***Lophocolea***

Class **MARCHANTIOPSIDA** CRONQUIST, TAKHT. & W. ZIMM.

Marchantiopsida Cronquist, Takht. & W. Zimm., Taxon **15**: 132. 1966 [“Marchantiatae”]. – Subclass Marchantiidae Schiffn. *in* Engl. & Prantl, Nat. Pflanzenfam. **1**(3): 1, 5. 1893 [“Marchantiales”]. – TYPE: *Marchantia* L. emend. Raddi.

Liverworts consititute a distinct and well-defined group of land plants characterised by an independent, haploid and potentially fertile gametophyte phase which regularly alternates with a dependent sporophyte phase producing haploid spores. They share these general features with mosses and hornworts with which they are unified in a separate division, Bryophyta, comprising three separate classes, Marchantiopsida or Hepaticopsida (Hepaticae, liverworts), Bryopsida (Musci, mosses) and Anthocerotopsida (Anthocerotae, hornworts) (Schuster, 1984). Recently some authors, for example Stotler and Crandall-Stotler (1977), Bartholomew-Began (1990) and Perold (1999), consider liverworts as a separate division, Hepatophyta, or Marchantiophyta (Crandall-Stotler & Stotler, 2000), parallel to Bryophyta and Anthocerotophyta.

The name of this group has an ancient origin when it was believed that various plants were marked by the Creator to identify the ailments they could cure. Because some thallose liverworts were considered to resemble the human liver, these plants were considered useful in curing liver ailments and this traditional belief survived in their common name “liver-plants” or liverworts. However, so far, no curative properties of liverworts have been confirmed and, additionally, most plants now aligned to this group are leafy and bear no resemblance to a liver!

Liverworts are a diverse assemblage of plants which are unified by the presence of elaters among spores (occasionally lacking, for example in *Riccia*) and unicellular, hyaline or pigmented rhizoids which are only occasionally lacking (in

Haplomitrium) as well as by the absence of a columella and stomata. The protonema is much reduced to two or three cells of the uniseriate germ tube and generally it gives rise to a single adult gametophyte. It is strongly chlorophyllose with numerous small chloroplasts which may be very rarely missing (in the saprophytic *Cryptothallus*). The gametophore may be either thallose or leafy with leaves arranged in two or three rows. The lateral leaves are usually in two rows and the third row, if present, is on the underside of the stem. These underleaves (amphigastria) often differ in size and shape from the lateral leaves. The leaves are mostly unistratose and lack a costa and they may be simple or lobed. Oil-bodies are a unique feature of hepatics, but their function still remains unknown. They occur in living cells in many genera, but usually disappear quite rapidly in dried plants. The gametophores often produce gemmae.

Over 90% of liverworts worldwide are dioecious. The sporophytes generally persist for a very short period after the spores are shed. They develop singly or in small groups in each perianth, which is a tube surrounding a developing sporophyte derived through the fusion of two or three leaves or, occasionally, from thallus tissue (e.g. in the Metzgeriales). The calyptra is ruptured and remains at the base of the seta when it elongates rapidly and protects the maturing sporangium before seta elongation. The sporangium usually opens by four longitudinal slits. The cells of the sporangium wall usually have nodular thickenings on the radial walls, and semi-annular thickenings on the inner or innermost tangential walls. The endothecium gives rise to spores which are free and unicellular, or sometimes remain in tetrads or become multicellular prior to dehiscence. Elaters are simple or occasionally branched and contain one to four spiral bands throughout their whole length.

The most comprehensive and exhaustive account of all aspects of Hepaticae is that of Schuster (1966) in the first volume of his monograph *The Hepaticae and Anthocerotae of North America east of the hundredth meridian*. His original concepts regarding evolution, phylogeny and classification of these plants were later developed in subsequent publications (Schuster, 1979*a*, 1984). General aspects of the structure and life-cycle of liverworts are described in some detail in many textbooks, of which the most useful are *Structure and life of bryophytes* (Watson, 1967) and *Introduction to bryology* (Schofield, 1985).

The class Marchantiopsida consists of approximately 6000 species worldwide (Schuster, 1966). They are classified in 349 genera which are assigned to 72 different families (Grolle, 1983*a*; Yano & Gradstein, 1997). Of these, only 27 species belonging within 19 genera and 12 families are presently known to occur in Antarctica. The class is usually subdivided into two subclasses, Jungermanniidae and Marchantiidae, which show the two main divergent evolutionary lines, but the features of these subclasses overlap to a certain degree. The Marchantiopsida are further subvided into five to seven orders which represent more detailed evolutionary trends in this class. Three orders are represented in the Antarctic.

KEY TO THE ORDERS OF MARCHANTIOPSIDA

1. Plants foliose (thallus divided into stem and leaves) . . . . **1. Jungermanniales**
1. Plants thalloid **2**
    2. Thallus translucent, lacking photosynthetic tissue and composed from one type of tissue . . . . **2. Metzgeriales**
    2. Thallus opaque, differentiated into photosynthetic tissue (with air chambers and air pores) and parenchymatic ventral tissue . . . . **3. Marchantiales**

Order I. JUNGERMANNIALES H. KLINGGR.

Jungermanniales H. Klinggr., Höh. Crypt. Preuss.: 10. 1858 ["Ordn. Jungermannieae"]. – TYPE: *Jungermannia* L.

Plants leafy or exceptionally (in non-Antarctic genera) thallose, usually dorsiventral with 2 rows of lateral leaves and 1 row of ventral underleaves. *Rhizoids* scarce to numerous, smooth, simple of branched. *Lateral leaves* horizontal to vertical, transversely to obliquely or arcuately inserted, asymmetrical or symmetrical, basically bilobed, arising from 2 meristematic cells, entire by infilling of sinus or sometimes 3–4(–5)-lobed by the activity of additional meristematic cells, unistratose or occasionally bi- to polystratose; leaf cells hexagonal, rounded or angular, isodiametric to elongate, smooth or with cuticular thickenings, with many small chloroplasts and various numbers of usually colourless oil bodies. *Underleaves* absent or similar to lateral leaves, this resulting in isophyllous shoots or, most often, dissimilar to lateral leaves, large to very small, making the shoots anisophyllous. *Gynoecia* terminal on main axes or on lateral-intercalary or ventral-intercalary branches, sometimes with subgynoecial innovations. Developing *sporophyte* usually protected by tubular perianth derived from modified fused leaves; seta anatomically undifferentiated or consisting of a limited number of cells; capsule globose to cylindrical, exserted on seta, uniformly 4-valved with 2–10-stratose walls. *Spores* unicellular and pigmented or multicellular and green; elaters free with 1–3(–4)-spiral, strongly pigmented spiral bands; elaterophores consistently absent.

The Jungermanniales are the largest order containing more than three fourths of all known liverworts (and 85% of the species known from Antarctica). There are 43 families, at least 280 genera and approximately 5000 species. They are distributed throughout the world from frigid climates into the humid tropical climates. Most species grow in moist environments, but there are some species which can tolerate extreme dessication. They thrive on various substrata, from rock and mineral soil to humus, many are epiphyllous or epiphytic on woody plants or sometimes on other bryophytes, and some are aquatic plants. The taxonomic and phylogenetic problems in this order have been discussed by Schuster (1972*b*).

It is very difficult, and in practice impossible, to prepare a key to the families using only gametophyte characters. Sporophyte characters are necessary for separation of families such as Cephaloziaceae and Cephaloziellaceae which differ only in cross-section of the seta. Because the vast majority of Antarctic populations are sterile, a key based on sporophyte characters would be very impractical and is not attempted here.

Family **I. HERBERTACEAE** MÜLL. FRIB. *ex* FULFORD & HATCHER

Herbertaceae Müll. Frib. *ex* Fulford & Hatcher, Bryologist **61**: 284. 1959 ["1958"]. – TYPE: *Herbertus* Gray, *nom. cons.*

Plants medium-sized to large, isophyllous to subisophyllous, yellowish-green, yellowish-brown, brown to reddish-brown, sometimes blackish, in loose mats to cushion-like turves. *Stem* rigid, suberect or erect, simple or with terminal (*Frullania*-type), lateral-intercalary (*Plagiochila*-type) or ventral-intercalary (*Bazzania*-type) branches, the latter type of branching producing mostly microphyllous flagellae; cortex 2–3-stratose, consisting of smaller, thick-walled cells surrounding thin-walled internal cells with small trigones. *Rhizoids* restricted mostly on the basal portion of the stem, hyaline. *Lateral leaves* slightly succubously to subtransversely inserted, ± falcate, bifid or trifid to 0.3–0.8 of the length into triangular to lanceolate-triangular lobes; leaf cells strongly collenchymatous, with distinct trigones, rarely not collenchymatous. *Underleaves* similar to lateral leaves in shape and size or sometimes only slightly smaller. *Dioecious* but mostly sterile. *Androecia* becoming intercalary; male bracts saccate, with 2–3 antheridia with biseriate stalk; bracteoles also with antheridia. *Gynoecia* terminal; female bracts similar to lateral leaves, only sometimes more dentate. *Perianth* deeply 3–6-plicate, deeply trilobed. *Calyptra* present, short. *Capsule* spherical; capsule wall 4–7-stratose, with outer layer with nodular and inner layer with semiannular thickenings. *Spores* smooth to faintly verruculose; spore/elater width ratio 2.0–2.5 : 1.

Only three genera, *Herbertus* Gray, *Olgantha* R. M. Schust. and *Triandrophyllum*, belong within this family (Grolle, 1983*a*). *Herbertus* is a large genus with very complicated taxonomy, distributed predominantly in wet mossy forests in tropical and, less often, in temperate areas. It consists of about 75 species but the actual number of species is difficult to evaluate because of the lack of critical taxonomic treatments in many areas. In southern South America it is represented by a single species, *H. runcinatus* (Taylor) Herzog, widespread in the *Nothofagus* zone (Fulford, 1963*a*; Engel, 1978). *Triandrophyllum* is the only representative of the family in the Antarctic. A taxonomic treatment of the Herbertaceae for Latin America was presented by Fulford (1963*a*).

1. **TRIANDROPHYLLUM** FULFORD & HATCHER

Triandrophyllum Fulford & Hatcher, Bryologist **64**: 349. 1962 ["1961"]. – HOLOTYPE: *Triandrophyllum subtrifidum* (Hook. f. & Taylor) Fulford & Hatcher (*Jungermannia subtrifida* Hook. f. & Taylor).

Plants subisophyllous, medium-sized to large, growing in loose mats, tufts or cushions, yellowish-brown, brown to somewhat reddish-brown. *Stems* simple or with ventral-intercalary, lateral-intercalary or, very rarely, terminal branches; cortex 1–2-layered, consisting of small cells with incrassate and mostly brownish walls surrounding thin-walled medullary cells with small trigones. *Rhizoids* very rare or absent. *Lateral leaves* asymmetric, with cordate dorsal or both bases, (bi-) or trifid to 0.2–0.5 of the length; segments acute, triangular, sometimes with dentate margins; leaf cells small, rotundate-quadrate to slightly hexagonal, thin- to slightly thick-walled; trigones nearly absent; cuticle smooth to papillose. *Underleaves* similar to lateral leaves, but slightly smaller. *Dioecious*. *Androecia* becoming intercalary on the main axis or lateral-intercalary on branches; male bracts and bracteoles similar to leaves, somewhat more saccate, bearing 2–3 antheridia in the axils of both bracts and bracteoles. *Gynoecia* terminal on the main stem or lateral-intercalary branch; bracts and bracteoles similar to leaves, but slightly larger. *Perianth* oblong-ovate, with 3–5 folds, contracted to the mouth. *Capsule* ovoid, with a 4–5-stratose wall.

Triandrophyllum is a small austral genus consisting of four species occurring primarily in the temperate regions of South America and Australasia and penetrating into the tropics in the northern Andes and Malesia. It was established by Fulford and Hatcher (1958) but the name was then invalidly published and not validated by these authors until three years later (Fulford & Hatcher, 1961). Initially the genus accommodated five species but later Fulford and Hatcher (1961) reduced *Triandrophyllum durum* (Steph.) Fulford & Hatcher and *T. antarcticum* Fulford & Hatcher to synonymy with *T. trifidum*. In addition, Solari (1973) considered *T. georgiense* (Steph.) Fulford & Hatcher to be conspecific with *T. subtrifidum* and reduced *T. trifidum* (Gottsche) Fulford & Hatcher to a variety of *T. subtrifidum*, transferring *T. durum* and *T. antarcticum* to the type variety. The additional species of this genus accepted are: *T. fernandeziense* (S. W. Arnell) Grolle from the Juan Fernandez Islands, based on *Acromastigium fernandeziense* S. W. Arnell (Grolle, 1961), *T. heterophyllum* (Steph.) Grolle from Java and New Guinea (Grolle, 1964) and the recently described *T. symmetricum* Engel from New Zealand (Engel, 1999). Additionally, Winkler (1976) described *T. maegdefraui* S. Winkl. from Colombia but this species proved to be conspecific with *Isotachis lacustris* Herzog (Uribe & Gradstein, 1998; Gradstein, 1999). Schuster (2000) accepted five taxa in this genus including four species (*T. heterophyllum*, *T. subtrifidum*, *T. georgiense* and *T. fernandeziense*), as well as an undescribed species from New Zealand, *T. falcifolium* R. M. Schust.

1. ***Triandrophyllum subtrifidum*** (HOOK. F. & TAYLOR) FULFORD & HATCHER

FIG. 21

Triandrophyllum subtrifidum (Hook. f. & Taylor) Fulford & Hatcher, Bryologist **64**: 350. 1962 ["1961"]. – *Jungermannia subtrifida* Hook. f. & Taylor, London J. Bot. **3**: 579. 1844. – *Isotachis subtrifida* (Hook. f. & Taylor) Mitt. *in* Hook. f., Fl. Nov. Zelandiae **2**(2): 148. 1854. – TYPE: Van Diemen's Land [HOLOTYPE: "Jungermannia subtrifida, Tayl. Van Diemen's Land. Lawrence 72 J. D. Hooker June 1844" – FH-TAYLOR!; ISOTYPE: BM!].

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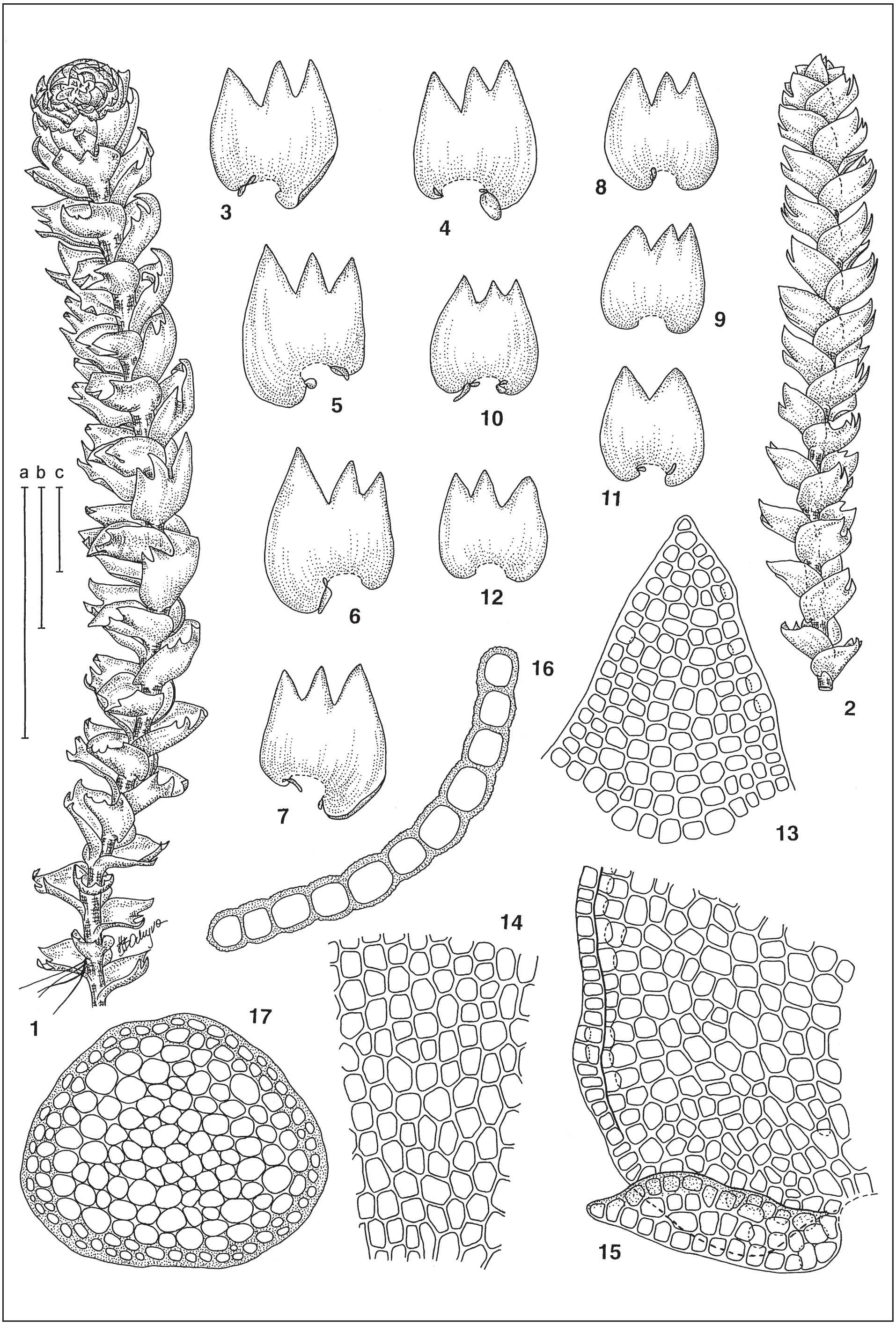
FIGURE 21. *Triandrophyllum subtrifidum*. **1**. Sterile shoot, ventral view. **2**. Sterile shoot, dorsal view. **3–7**. Leaves. **8–12**. Underleaves. **13**. Apex of lobe. **14**. Basal cells in the middle part of leaf. **15**. Angular cells of leaf. **16**. Transverse section of leaf lobe, note small cuticular roughness. **17**. Transverse section of stem. (All from *Holdgate 832B*, AAS.) Scale bars: a – 5 mm (1–2); b – 1 mm (16); c – 1 mm (3–12) and 100 µm (13–15, 17).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Plants medium-sized to large, brownish or yellowish-brown, reddish at the tips, in loose or dense mats or tufts. *Stems* 2–4(–6) cm long, erect or ascending, simple or lateral-intercalary branched, with flagelliform ventral-intercalary branches; cortical cells in 1–2 layers, small, thick-walled surrounding 10–15 layers of thin-walled internal cells with trigones. *Leaves* loosely imbricate below, becoming approximate toward the stem tips, spreading, asymmetric and falcate, 1–2 mm long, 0.6–1.7 mm wide, ovate, oblong-ovate to ovate-truncate, trifid or rarely bifid to 0.3–0.5 of their length, postically secund; margins entire or dentate at the base; segments triangular to lanceolate, equal or with the dorsal segment mostly larger, acute to bluntly subacute, 14–18 cells wide at the base; leaf cells subquadrate to subhexagonal, thin-walled or slightly thick-walled, without or with small trigones, 25–30 × 25–35 μm; cuticle smooth to verruculose. *Underleaves* of the same size and shape as the lateral leaves or rarely slightly smaller. *Sterile* in Antarctica.

Taxonomic and nomenclatural notes. — The species was originally described by Hooker and Taylor (1844) as *Jungermannia subtrifida* Hook. f. & Taylor from Tasmania on the basis of specimens collected by J. D. Hooker during his Antarctic voyage in 1839–1843. The species is very variable; Solari (1973) and Hässel de Menendez and Solari (1975) listed 16 heterotypic synonyms of the type variety only. In addition, they recognised two other varieties of this species, var. *fuscum* (Steph.) Solari and var. *trifidum* (Gottsche) Solari, both widely distributed in the *Nothofagus* zone in southern South America, and the latter also having some isolated stations in the Andes of Colombia and Bolivia.

Differentiation. — The species is very distinct since it is the only subisophyllous species in Antarctica with trilobed, slightly falcate leaves.

Reproduction in Antarctica. — Fertile plants unknown.

Habitat. — On soil, volcanic debris, on rock under rock ledges and on gravel, usually in sheltered situations.

World range. — An imperfectly south-pan-temperate species, occurring principally in New Zealand and Tasmania and in southern South America from Tierra del Fuego extending north to the Valdivian region (Solari, 1973; Hässel de Menendez & Solari, 1975; Engel, 1978), on the Falkland Islands (Engel, 1990*a*) and South Georgia (Grolle, 1972*a*; Solari, 1973; Hässel de Menendez & Solari, 1975); its occurrence on Tristan da Cuhna (Arnell, 1958) completes its pan-temperate range (Fig. 22, inset). Additionally, it penetrates into the tropics along the Andean chain, from Peru to Guatemala and an isolated station is known from the Philippines (Kitagawa, 1981).

Distribution in Antarctica. — The species appears to be rare in the Antarctic, being known only from the South Sandwich Islands, where it is occasionally abundant (Fig. 22). Until recently it was known only from Leskov Island, but it is reported here for the first time from Candlemas Island.

Specimens examined. — SOUTH SANDWICH ISLANDS. **LESKOV ISLAND**. Summit ridge, 100 m, *Convey 245B, 246E, 247F & 250D* (AAS, KRAM) and 200 m, *Longton 484, 485A,*

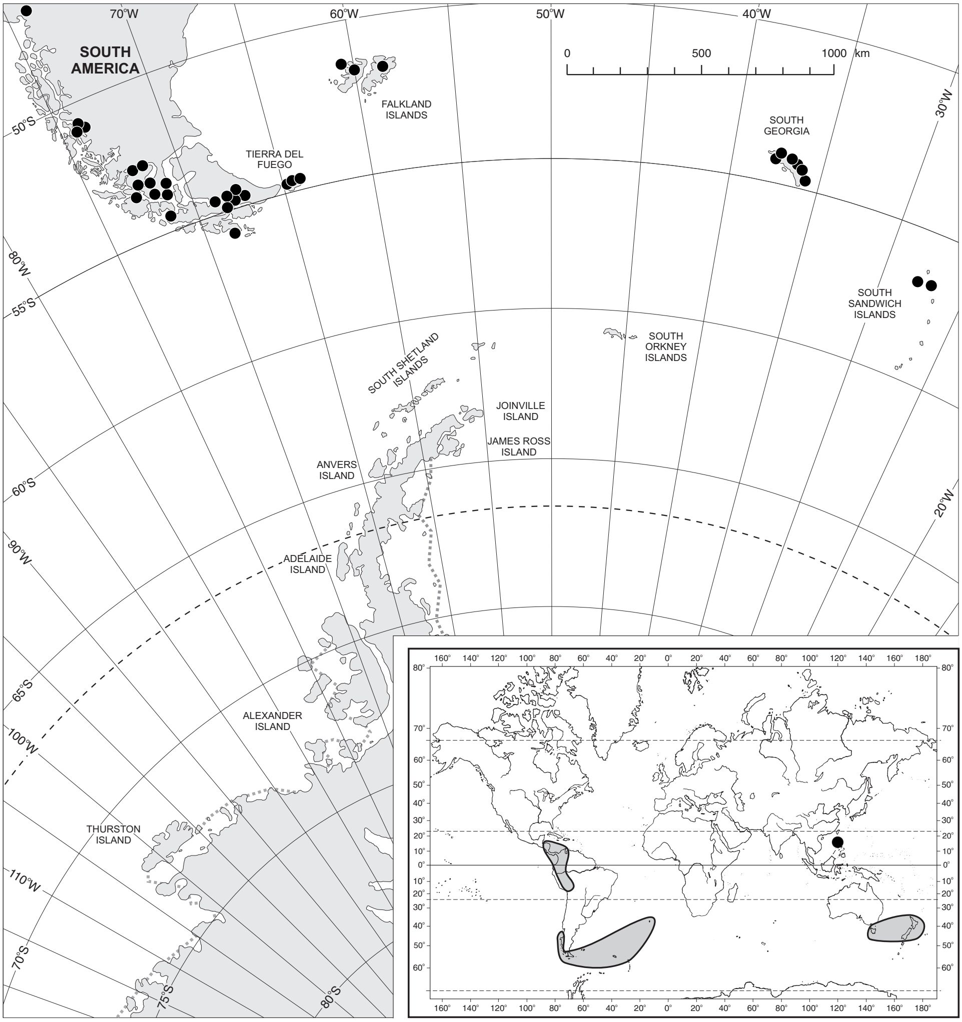

FIGURE 22. Distribution of *Triandrophyllum subtrifidum* in the Antarctic and Fuegian region. Inset: global distribution.

486, 487A, 500A, 502B, 503, 504, 507A & 509A (AAS, KRAM) and *Holdgate 832B* (AAS, KRAM). **CANDLEMAS ISLAND.** Lucifer Hill, south edge of shallow gully above Clinker Gulch, *Convey 124C, 125C & 126C* (AAS, KRAM).

Literature records. — SOUTH SANDWICH ISLANDS: without indication of the island (Lewis Smith, 1993: 322); Leskov Island (Grolle, 1972*a*: 85; Longton & Holdgate, 1979: 11; Lewis Smith, 1979*b*: 60; Ochyra & Váňa, 1989*b*: 214); Candlemas Island (Convey *et al.*, in press).

Family **II. LEPIDOZIACEAE** LIMPR.

Lepidoziaceae Limpr. *in* Cohn, Kryptogamen-Fl. Schlesien **1**: 310. 1877 [“Lepidozieae”]. – TYPE: *Lepidozia* (Dumort.) Dumort., *nom. cons.*

Plants minute to medium-sized or large, prostrate, ascending or erect. *Stems* soft or rigid, usually opaque, with a unistratose cortex, simple or more commonly freely 1–2(–3)-pinnately or pseudodichotomously branched; branches mostly terminal (*Frullania*-type, rarely *Microlepidozia*- or *Acromastigium*-types), lateral-intercalary (*Plagiochila*-type) or ventral-intercalary (*Bazzania*-type), the last producing microphyllous stolons, furcate or pinnate and sometimes becoming attenuate and flagelliform. *Rhizoids* fasciculate, arising from the base of underleaves, rarely some scattered on the ventral surface of the stem. *Leaves* incubous, obliquely inserted or less often transverse, rarely ± succubous, mostly unistratose, sometimes also polystratose, unlobed to most often 2–4(–12)-lobed or dentate with sinuses acute or rounded, lobes entire, often long and slender. *Underleaves* as wide as stem to much wider, 0.2–0.9 of the length of lateral leaves, rarely vestigial, similar in shape to lateral leaves. *Gemmae* unknown. *Monoecious* (autoecious) or *dioecious*. *Androecia* on postical branches, rarely terminal on elongated branches; male bracts similar to lateral leaves, smaller and saccate at base; bracteoles large, without antheridia; antheridia 1–2 per bract, with 1–2-seriate stalk. *Gynoecia* on abbreviated ventral-intercalary branches, rarely terminal on lateral branches; bracts larger than the lateral leaves leaves; bracteoles similar to bracts. *Perianth* ovoid to fusiform, cylindrical and mostly polystratose below, unistratose and trigonous above, gradually tapering distally. *Seta* with 8–16 epidermal cells surrounding (4–)12 to numerous rows of narrower inner cells. *Spores* papillose, verrucose to areolate; elaters bispiral; spore/elater width ratio mostly 1.0–1.5(–2.5) : 1.

The Lepidoziaceae are a very large, primitive and heterogeneous family which is mainly Gondwanalandic in range (Schuster, 1982). It comprises 28 genera subdivided into seven subfamilies (Grolle, 1983*a*), and Schuster (1984, 2000) added an eighth subfamily (Drucelloideae). The majority of genera (often ill-defined) and species, as well as four subfamilies, occur exclusively in tropical and temperate regions in the Southern Hemisphere. The number of species in the Northern Hemisphere is low and they occur mainly in temperate to subarctic regions. The total number of species in the Lepizodiaceae is difficult to assess because some large genera, such as *Bazzania* and *Lepidozia*, are still imperfectly known taxonomically. Three species belonging within two genera, which are distinguished in the following key, are known from the Antarctic.

KEY TO THE ANTARCTIC GENERA OF THE LEPIDOZIACEAE

1. Leaves unlobed to at least emarginate at the apex .... **1. *Hygrolembidium***
1. Leaves (3–)4-lobed .... **2. *Lepidozia***

1. HYGROLEMBIDIUM R. M. SCHUST.

Hygrolembidium R. M. Schust., J. Hattori Bot. Lab. **26**: 277. 1963. – HOLOTYPE: *Hygrolembidium isodictyon* (Herzog) R. M. Schust. (*Lembidium isodictyon* Herzog) [=*Hygrolembidium acrocladum* (Berggr.) R. M. Schust.].

Plants relatively small, green to pale green or whitish. *Stems* soft or ± fleshy, without a hyalodermis or thick-walled cortical cells, erect, simple or lateral-intercalary or ventral-intercalary branched, sometimes with long, slender, prostrate and freely branched stolons. *Rhizoids* scattered on the ventral side of stem, rarely in small fascicles arising from the underleaf bases. *Leaves* concave to cupulate, fleshy, succubously or transversely inserted, unlobed to slightly retuse or shallowly bilobed, at least at base 2–7-stratose; leaf cells thin-walled or sometimes equally thick-walled, without trigones, with a smooth to slightly papillose cuticle. *Underleaves* distinct, small to almost the same size as lateral leaves, unlobed to shallowly bilobed. *Gemmae* absent. *Dioecious*. *Male plants* much smaller than female plants; androecia spicate, on ventral-intercalary branches; male bracts much smaller than leaves, strongly saccate, bearing 1–4 antheridia with 2–4 or more seriate stalks; bracteoles present, without or with occasional (in *H. australe*) antheridia. *Gynoecia* on short intercalary branches lacking normal leaves; female bracts bifid to lobulate. *Perianth* 2–5-stratose at base, mostly unistratose and trigonous at least above, contracted to the crenulate to lobate mouth. *Seta* with 10–20 large external cells surrounding many rows of smaller internal cells. *Capsule* wall 3–5-stratose; epidermal cells with nodular thickenings, the innermost cells with nodular or imperfect semiannular thickenings. *Spores* papillose; spore/elater width ratio 1.5–2.5 : 1.

A small genus comprising eight species divided into two subgenera and three sections (Schuster & Engel, 1987) belonging (together with three other genera, *Isolembidium*, *Lembidium* and *Chloranthelia*), to subfamily Lembidioideae which is strictly Gondwanalandic in distribution. Grolle (1983*a*) placed in this subfamily the monotypic genus *Austrolembidium* Hässel from South Georgia but Schuster (2000) considered it to be congeneric with *Evansianthus*. *Hygrolembidium* is confined in its distribution to the southern cool temperate, subantarctic and antarctic region, including New Zealand, Tasmania, south-east Australia, some periantarctic islands, Tierra del Fuego, southern and central Chile and the northern maritime Antarctic. Only one or two species penetrate northwards to high elevations in the tropics, namely *H. boschianum* (Sande Lac.) R. M. Schust. which is known from Sri Lanka, Java and New Guinea, and probably *H. andinum* Herzog which is known from Central Chile and from a fragmentary collection of uncertain identity from the northern Andes of Venezuela (Schuster & Engel, 1987). Two species of *Hygrolembidium* classified in two different subgenera are known from Antarctica. They may be differentiated by the following couplet.

KEY TO THE ANTARCTIC SPECIES OF *HYGROLEMBIDIUM*

1. Plants subisophyllous to isophyllous; underleaves large, entire; slime papillae at leaf and underleaf margins present . . . . **1. *H. isophyllum***
1. Plants anisophyllous; underleaves small, slightly bilobed; slime papillae at leaf and underleaf margins absent . . . . **2. *H. ventrosum***

1. *Hygrolembidium isophyllum* R. M. SCHUST. FIG. 23

Hygrolembidium isophyllum R. M. Schust., Nova Hedwigia **15**(2–4): 467, *pl. 56(8), f. 1–9*. 1968. – TYPE: Argentina, Tierra del Fuego, Cerro Garibaldi near Lago Escondido, *RMS 58319e* [HOLOTYPE: Hb. Schuster (*non vidi*)].

Plants small to medium-sized, mostly densely caespitose, julaceous, isophyllous or nearly so, whitish to yellowish-green. *Stems* 5–15 mm long, erect to ascending, simple or more commonly lateral-intercalary or ventral-intercalary branched, occasionally with rhizoidal, microphyllous stolons, in transverse section with numerous rows of thin- or slightly firm-walled cortical cells, 25–35 µm wide, surrounding 8–11 layers of somewhat larger, thin-walled medullary cells, 30–40 µm wide. *Rhizoids* mostly restricted to the base of leafy shoots, arising from bases of underleaves or from leafless parts of stem. *Leaves* contiguous to closely imbricate, pellucid, delicate, strongly concave to cupulate, reniform, broadly cordate, suborbicular to broadly orbicular-ovate, 0.5–0.6 mm long, 0.4–0.5 mm wide, unistratose or rarely 2(–3)-stratose only in median and basal parts, obtuse, rounded-truncate to retuse or emarginate, never distinctly lobed at the apex; margins entire, with 5–20 slime papillae; leaf cells quadrate to subquadrate, 25–30 × 25–35 µm, with thin or slightly thickened walls, without trigones, marginal row of cells sometimes tangentially elongate, cuticle smooth. *Underleaves* similar to lateral leaves in shape and size or only slightly narrower. *Sterile.*

Taxonomic and nomenclatural notes. — *Hygrolembidium isophyllum* was described from a collection consisting of only two sterile shoots from Paso Garibaldi on Isla Grande de Tierra del Fuego (Schuster, 1968*a*). Later Engel (1974) described and illustrated fertile plants of the species from the Brunswick Peninsula, confirming its placement in *Hygrolembidium*. Because it occupies an isolated position in *Hygrolembidium*, Schuster (1968*a*) placed it in the separate subgenus *Hygrobiellopsis* R. M. Schust. This alignment was subsequently accepted in a monograph of this genus by Schuster and Engel (1987) who added to this subgenus two species from New Zealand, *H. triquetrum* R. M. Schust. & J. J. Engel and *H. rigidum* R. M. Schust. & J. J. Engel. The latter two species were placed in sect. *Rigidi* R. M. Schust. & J. J. Engel, whereas *H. isophyllum* was retained in sect. *Hygrobiellopsis*. Unfortunately, when recognizing this subgenus Schuster (1968*a*) failed to provide a Latin description of this taxon because he stated that the Latin diagnosis of the species may simultaneously validate the subgeneric name. However, according to Art. 42.1 (Greuter *et al.*, 1994) *descriptio generico-specifica* may serve for validation of generic names only, not infrageneric taxon names (subgenus, section, etc.). Accordingly, this name is validated here.

Hygrolembidium R. M. Schust. subgen. ***Hygrobiellopsis*** R. M. Schust. [R. M. Schust., Nova Hedwigia **15**(2–4): 467. 1968, *nom. inval.*: Art. 32.1 + 41.2].

Plantae isophyllae vel subisophyllae, amphigastriis eadem ac foliis lateralibus simillimis vel saltem 0.4 folii magnitudinis et marginibus foliorum papillis mucosis praeditis facile dignoscenda. Type species: *Hygrolembidium isophyllum* R. M. Schust.

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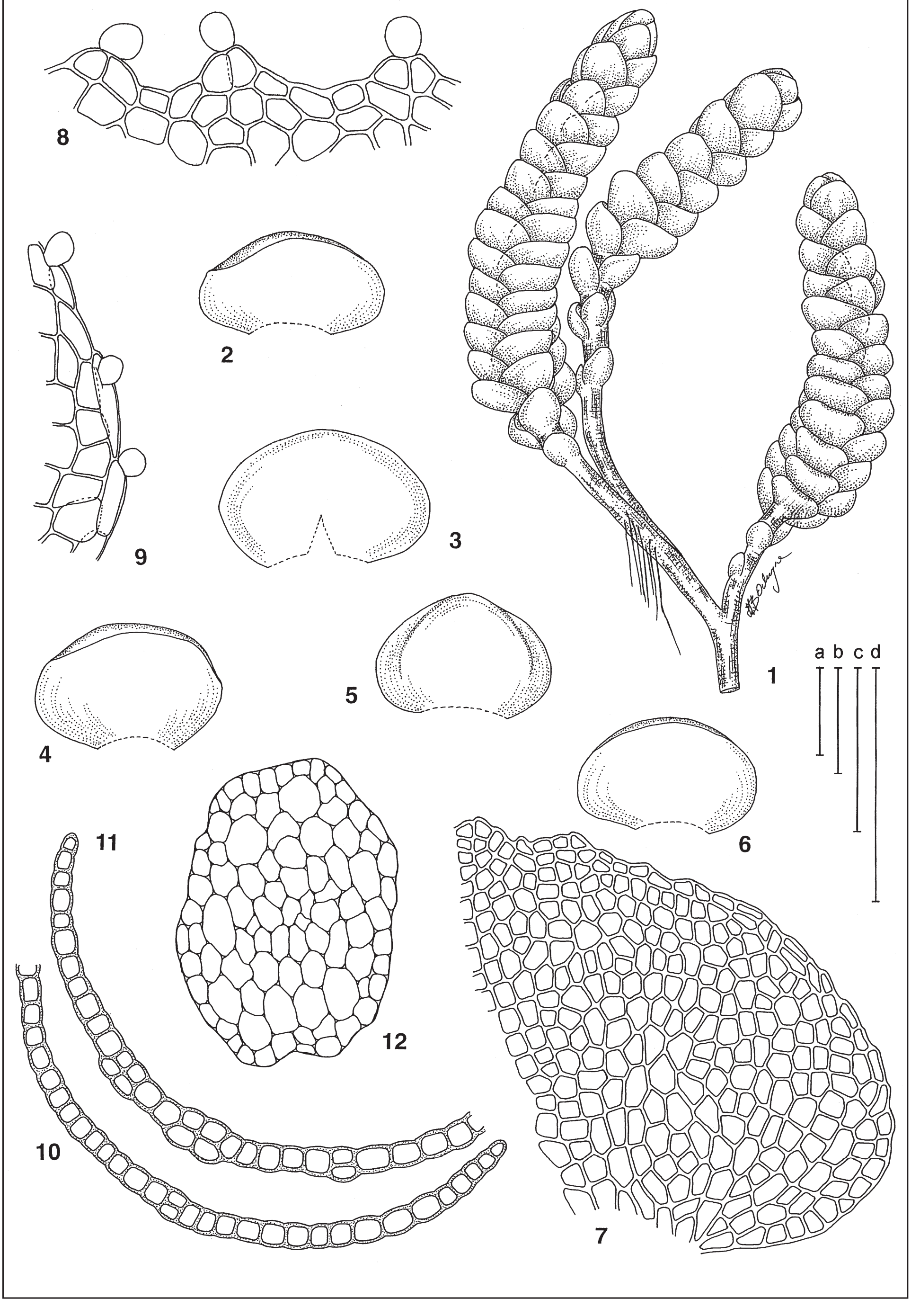
FIGURE 23. *Hygrolembidium isophyllum*. **1**. Sterile shoot. **2–4**. Leaves. **5–6**. Underleaves. **7**. Laminal cells. **8**. Leaf apex with slime papillae. **9**. Leaf margin with slime papillae. **10–11**. Transverse section of leaf in lower quarter. **12**. Transverse section of stem. (All from *Ochyra 2500/80*, KRAM.) Scale bars: a – 100 µm (7, 10–12); b – 1 mm (1); c – 100 µm (8–9); d – 1 mm (2–6).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Differentiation. — *Hygrolembidium isophyllum* is a distinct species which is unlikely to be mistaken for any other species in the Antarctic. The strongly concave, densely imbricate and isophyllous or subisophyllous lateral leaves and amphigastria give the shoots a unique stoutly julaceous aspect. Moreover, the mostly unistratose leaves with subquadrate cells lacking trigones and the presence of the slime papillae at the leaf and underleaf margins are useful microscopic characters which enable identification of the species.

Reproduction in Antarctica. — Fertile plants unknown.

Habitat. — This species occurs mainly in moist habitats. It grows amongst mosses and over soil, on gravelly or stony ground, in seepage and flushed areas, on slopes, amongst boulders, stones and rocks, on cliff scree, below late snow patches, at margins of runnels and on frost-heaved stones. These habitats are generally dominated by fruticose lichens and cushion mosses (e.g. *Andreaea* spp., *Bartramia patens*, *Ceratodon purpureus*, *Dicranoweisia brevipes*, *Notoligotrichum trichodon*, *Polytrichastrum alpinum*, *Racomitrium sudeticum*, *Warnstorfia sarmentosa*). Occasionally it thrives on moist peat banks dominated by *Polytrichum strictum* and *Chorisodontium aciphyllum*.

World range. — An American subantarctic species known from the South Orkney and South Shetland Islands in West Antarctica, South Georgia (Hässel de Menendez, 1977), the Falkland Islands (Engel, 1990*a*), Tierra del Fuego (Schuster, 1968*a*; Schuster & Engel, 1987), Brunswick Peninsula (Engel, 1974, 1978) and extending to the vicinity of Puerto Natales at lat. *ca* 52°S in the Magellanian region of western Patagonia (Engel, 1973*a*, 1978) (Fig. 24). The species is here considered as a subantarctic rather than south-temperate element because its northward extensions from the Antarctic and Subantarctic to the Falkland Islands, Tierra del Fuego and mainland South America are at high or relatively high elevations.

Distribution in Antarctica. — A rare species, known only from the South Orkney and South Shetland Islands, but it is locally common on Signy Island. It occurs from sea level to 250 m, although most collections are from below 100 m (Fig. 25). The reports from Cape Tuxen on the Graham Coast on the west coast of the Antarctic Peninsula and on Powell Island in the South Orkney Islands (Ochyra & Váňa, 1989*b*) were based upon misidentifications.

Specimens examined. — SOUTH ORKNEY ISLANDS. CORONATION ISLAND. East side of Olivine Point, *ca* 15 m, *Lewis Smith 119* (AAS, KRAM); west side of Cape Hansen, 60 m, *Lewis Smith 5230* (AAS, KRAM); Cape Hansen, 20–250 m, *Lewis Smith 3240 & 3241* (AAS, KRAM). LYNCH ISLAND. North facing slope, *ca* 15 m, *Lewis Smith 531* (AAS, KRAM). SIGNY ISLAND. Factory Cove, *ca* 15 m, *Holdgate 58* (AAS, KRAM), *ca* 35 m, *Holdgate 51* (AAS, KRAM) and *Lewis Smith 475B & 495* (AAS, KRAM), 50 m, *Lewis Smith 5202* (AAS, KRAM), 75 m, *Lewis Smith 1841 & 5201C* (AAS, KRAM); Factory Bluffs, 80 m, *Lewis Smith 10930* (AAS, KRAM); between Factory Cove and Paal Harbour,

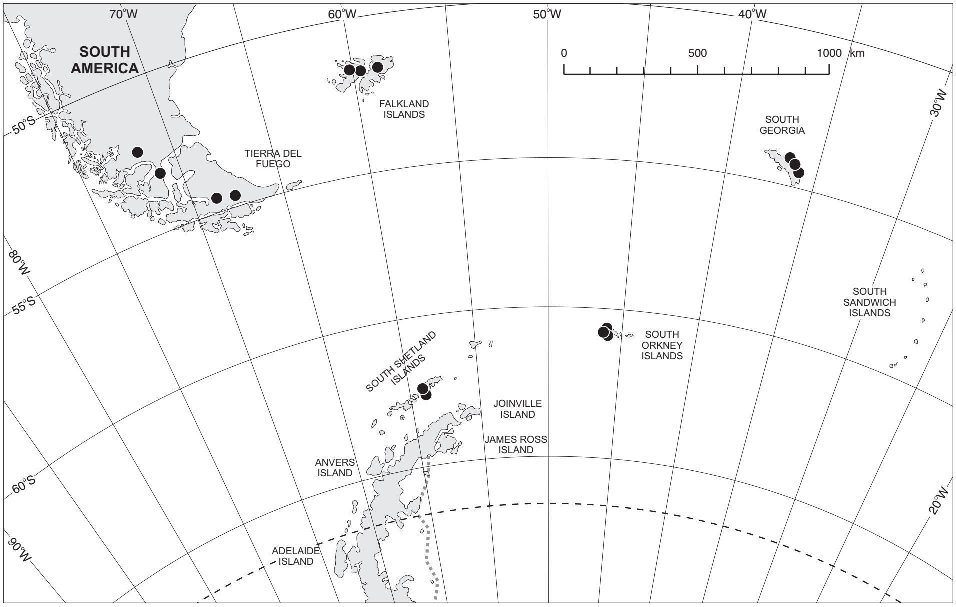

FIGURE 24. Global distribution of *Hygrolembidium isophyllum.*

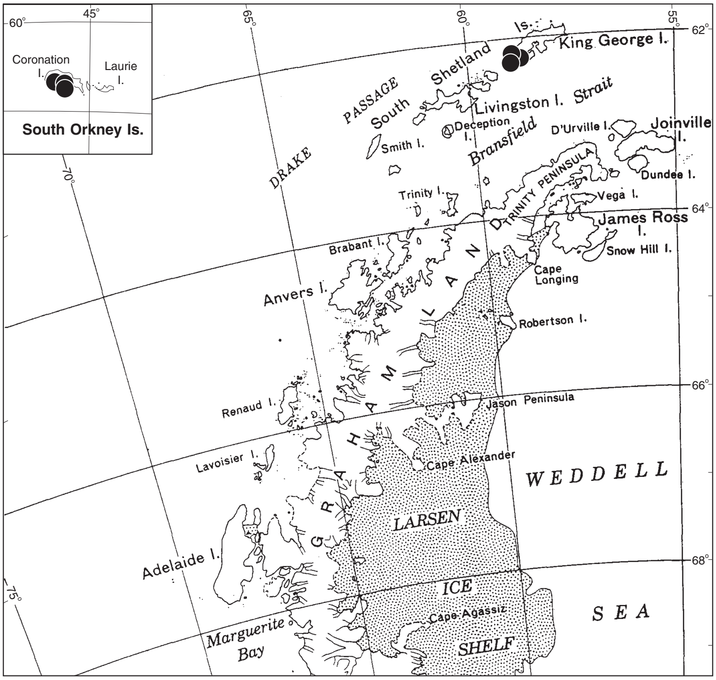

FIGURE 25. Distribution of *Hygrolembidium isophyllum* in the Antarctic.

ca 115 m, *Holdgate 28* (AAS, KRAM); Rethval Point, *ca* 50 m, *Holdgate 103B* (AAS, KRAM); Gneiss Hills, 200 m, *Lewis Smith 8112* (AAS, KRAM); Moraine Valley, 60 m, *Lewis Smith 5224* (AAS, KRAM), 65 m, *Lewis Smith 5205C* (AAS, KRAM) and 75 m, *Lewis Smith 10851* (AAS, KRAM); west side of Rusty Bluff, *ca* 50 m, *Lewis Smith 551A* (AAS, KRAM). **Moe Island**. Spaull Point, *ca* 100 m, *Lewis Smith 5240A* (AAS, KRAM).

SOUTH SHETLAND ISLANDS. **King George Island**. ***Fildes Peninsula***: Ardley Island, 5 m, *Ochyra 2500/80* (AAS, KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 75 (erroneously as *H. ventrosum*)]. **Nelson Island**. Without specific locality, *Komárková 90* (KRAM).

Literature records. — SOUTH ORKNEY ISLANDS. Coronation Island (Ochyra & Váňa, 1989*b*: 215); Lynch and Moe Islands (Bonner & Lewis Smith, 1985: 68); Signy Island (Lewis Smith, 1972: 19; Lewis Smith & Coupar, 1986: 194; Schuster & Engel, 1987: 302; Ochyra & Váňa, 1989*b*: 215). SOUTH SHETLAND ISLANDS. King George Island (Ochyra, 1984: 12 as *Hygrolembidium ventrosum*; Ochyra *et al*., 1986: 56; Schuster & Engel, 1987: 302; Ochyra & Váňa, 1989*a*: 193, 1989*b*: 215). WEST ANTARCTIC PENINSULA. Graham Coast (Ochyra & Váňa, 1989*b*: 215 – this record correctly refers to *Herzogobryum teres*).

2. *Hygrolembidium ventrosum* (Mitt.) Grolle FIG. 26

Hygrolembidium ventrosum (Mitt.) Grolle *in* Zinderen Bakker, Winterbottom & Dyer, Marion Prince Edward Is. S. Afr. Biol. Geol. Exp. 1965–1966: 233. 1971 [*Hygrolembidium ventrosum* (Mitt.) R. M. Schust., J. Hattori Bot. Lab. **26**: 277. 1963, *nom. inval.*]. – *Lembidium ventrosum* Mitt., J. Linn. Soc. Bot. **15**: 69. 1876. – Type: Kerguelen's Island, "inter *Psilopilum trichodium* Wils.", Challenger Exped., [Moseley s.n.] [Lectotype: NY–mitt!].

Plants small in compact mats or tufts, mostly yellowish, light yellow-green to whitish- green. *Stems* erect, to 0.5 mm high, simple to lateral-intercalary or ventral-intercalary branched, sometimes with long, slender stolons, in transverse section consisting of many rows of thin-walled cells, 15–30 × 25–35 μm, surrounding 8–10 rows of medulary cells, 30–40(–50) μm wide. *Rhizoids* relatively common, arising from the basal cells of underleaves or leaves and also scattered throughout the stem and branches. *Leaves* contiguous to closely imbricate, firm and rather rigid, firmly attached, suberect to obliquely spreading, slightly succubously to transversely oriented, deeply concave, orbicular to widely ovate, to 1.05 mm wide and to 0.95 mm long when flattened, in transverse section 2(–3)-stratose from the middle to the base; leaf cells subquadrate to subrectangular, with thickened walls and without trigones, 25–40 × 30–50 μm, slightly elongate near the base, smooth or nearly so. *Underleaves* small, often inconspicuous, plane to weakly concave, ovate, with 1–2 teeth or slightly bifid at the apex. *Dioecious*. *Gynoecia* on ventral-intercalary branches; bracts large, concave; bracteole linear to narrowly ovate. *Perianth* ovoid, 2–3-stratose at base, bistratose in the middle, unistratose and trigonous above, with a spinose-

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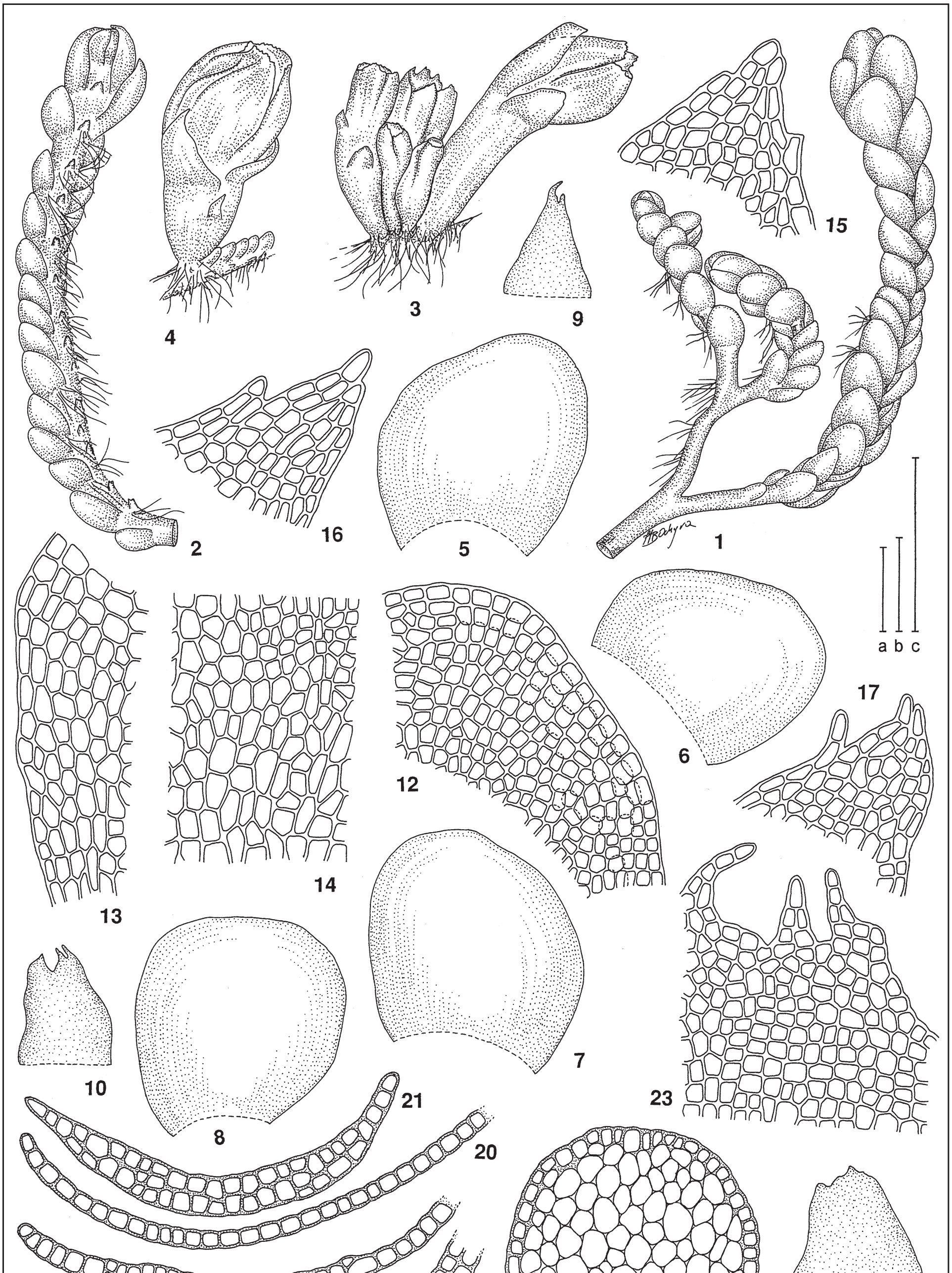
Figure 26. *Hygrolembidium ventrosum*. **1**. Sterile plant with one ventral-intercalary branch. **2**. Leafy branch in ventral-lateral view with perianth. **3–4**. Gynoecia. **5–8**. Leaves. **9–11**. Underleaves. **12**. Laminal cells at distal portion of leaf. **13**. Marginal cells at proximal portion of leaf. **14**. Mid-leaf cells. **15–17**. Areolation of underleaf. **18–21**. Transverse sections of leaf. **22**. Transverse section of stem. **23**. Portion of perianth mouth. (All from *Ochyra 2158/80*, KRAM.) Scale bars: a – 100 μm (12–23); b – 1 mm (1–4); c – 0.5 mm (5–8) and 1 mm (9–11).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dentate to lobulate mouth of elongate cells. *Androecia* and *sporophytes* unknown in Antarctic material.

Taxonomic and nomenclatural notes. — The species was originally described by Mitten (1876) as *Lembidium ventrosum* Mitt. from the material collected in 1874 on Îles Kerguelen by H. N. Moseley during the "Challenger" Expedition. Only the plants in the original Mitten herbarium in NY represent this species whereas the duplicate in BM is actually *Clasmatocolea vermicularis* (Lehm.) Grolle. Schuster (1963) was the first to transfer *L. ventrosum* to the newly established genus *Hygrolembidium*, but he did not cite the basionym in full, thus invalidly publishing the new combination. This transfer was correctly made by Grolle (1971*a*).

Differentiation. — The species is recognised by its undivided leaves which are polystratose in the lower half and small underleaves.

Reproduction in Antarctica. — Only female plants haved been recorded; male plants and sporophytes have not been observed.

Habitat. — Antarctic plants occur on slightly moist soil in a community dominated by *Usnea aurantiaco-atra* associated with *Andreaea regularis*, *Pohlia cruda* and *Polytrichastrum alpinum*.

World range. — An amphiatlantic subantarctic species, widely distributed in the South Indian Ocean Province (previously termed Kerguelen Biogeographical Province) including Îles Kerguelen (Mitten, 1876; Herzog, 1952*a*; Schuster & Engel, 1987), Marion Island (Grolle, 1971*a*; Schuster & Engel, 1987) and Îles Crozet (Schuster & Engel, 1987), and disjunctly in the South Orkney and South Shetland Islands in the northern maritime Antarctic (Fig. 27). The report from New Zealand (Stephani, 1906; Gibbs, 1911; Herzog, 1952*a*) is erroneous and the voucher specimens correctly belong to *Lembidium nutans* (Hook. f. & Tayl.) Mitt. or *Hygrolembidium acrocladum*.

Distribution in Antarctica. — This appears to be an exceedingly rare species, previously known only from King George Island (Ochyra and Váňa, 1989*a*, *b*) but here it is also reported from Signy Island and additional stations on King George Island (Fig. 28). It occurs at elevations from sea level to 135 m.

Specimens examined. — SOUTH ORKNEY ISLANDS. **SIGNY ISLAND**. Gneiss Hill south-east of Cummings Cove, *ca* 135 m, *Lewis Smith 620* (AAS, KRAM).

SOUTH SHETLAND ISLANDS. **KING GEORGE ISLAND**. ***Admirality Bay***: Mt. Wawel, 40 m, *Ochyra 2157/80 & 2158/80* (KRAM, PRC). ***Fildes Peninsula***: Ardley Island, *Nikolaev 32 p.p., 64 p.p.* (JE, LE), *71 p.p. & 72 p.p.* (LE, PRC); without closer locality data, Dec 1988, *Macchiavello s.n.* (BA).

Literature records. — SOUTH SHETLAND ISLANDS: King George Island (Ochyra, 1984: 12 – this record is correctly *Hygrolembidium isophyllum*; Ochyra & Váňa, 1989*a*: 193; 1989*b*: 215).

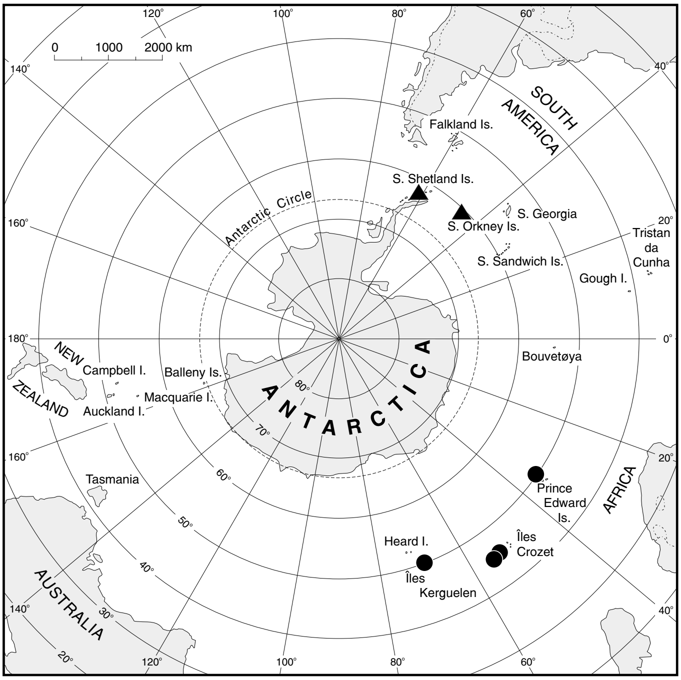

FIGURE 27. Global distribution of *Hygrolembidium ventrosum*. The Antarctic localities are indicated by triangles.

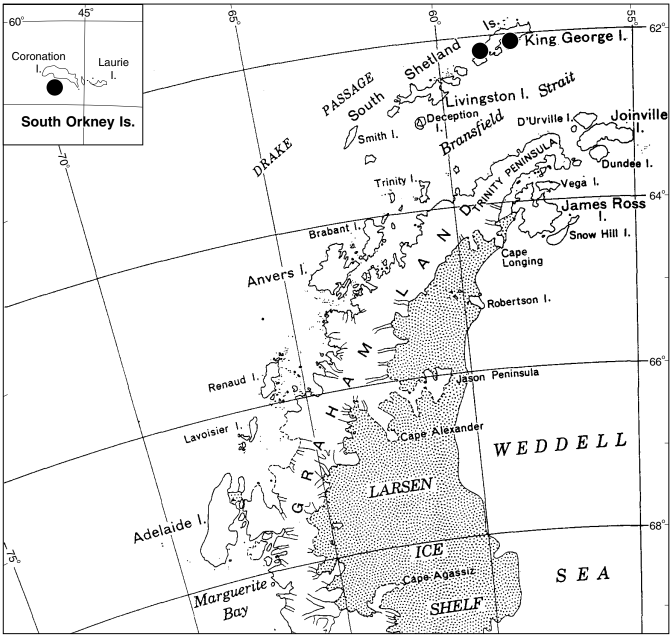

FIGURE 28. Distribution of *Hygrolembidium ventrosum* in the Antarctic.

2. LEPIDOZIA (DUMORT.) DUMORT.

Lepidozia (Dumort.) Dumort., Recueil Observ. Jung.: 19. 1835, *nom. cons.* – *Pleuroschisma* Dumort. sect. *Lepidozia* Dumort., Sylloge Jung. Eur. Indig.: 69. 1831. – TYPE (*cons.*): *Lepidozia reptans* (L.) Dumort. (*Jungermannia reptans* L.).

Plants minute to small or medium-sized, green, yellowish-green to brownish. *Stems* prostrate, procumbent to erect, pinnately to bipinnately branched, branching terminal, lateral-intercalary to ventral-intercalary; branches sometimes flagelliferous, microphyllous, with many rhizoids. *Rhizoids* with branched ends, arising at the bases of underleaves or along flagelliform branches. *Leaves* horizontal, incubous, asymmetric and mostly subquadrate, unlobed to (3–)4–5-lobed to 0.3–0.8 of the length; margins entire to slightly dentate; lobes mostly triangular-acuminate or subulate, decurved, unequal; leaf cells thick- to thin-walled, concave, with concave or mostly without trigones. *Underleaves* smaller than leaves but otherwise similar in shape, transversely inserted. *Monoecious* or *dioecious*. *Androecia* on short ventral branches, rarely terminal on lateral-intercalary branches; male bracts similar to leaves, concave. *Gynoecia* on short ventral lobes; bracts and bracteoles similar, larger than the leaves. *Perianth* cylindrical-fusiform, trigonous at least in the upper part. *Seta* of 12–14 rows of large epidermal cells surrounding numerous inner cells. *Capsule* ovoid with 3–8-stratose wall. *Spores* papillate.

A very large nearly cosmopolitan genus, with a particular concentration of species in montane rain forests in tropical and subtropical as well as in antipodal areas. Because *Lepidozia* is in need of taxonomic revision, the number of its species cannot be precisely given, although from over 300 species names combined with this generic name, less than half are probably valid. The genus is represented in Antarctica by a single species.

1. *Lepidozia chordulifera* TAYLOR FIG. 29

Lepidozia chordulifera Taylor, London J. Bot. **5**: 371. 1846. – *Jungermannia chordulifera* (Taylor) Taylor & Hook. f. *in* Hook. f., Fl. Antarct. **2**: 442. 1847. – *Mastigophora chordulifera* (Taylor) Trevis., Mem. Reale Ist. Lomb. Sci. Lett. Ser. 3, **4**: 397. 1877. – TYPE: [Chile] Chonos Archipelago, n. 461; Darwin, Hook. Herb. [HOLOTYPE: "Jungermannia chordulifera Tayl. (Lepidozea)" 461 Chonos Archipelago. Darwin "Hook. Hab. J. D. Hooker June 1844" – FH-TAYLOR!; ISOTYPE: BM–HOOK!].

Lepidozia cuspidata Steph., K. Svensk. Vet. Akad. Handl. **46**(9): 61, *f. 23a–b*. 1911. – TYPE: Westpatagonien – näheres über den Fundort nicht bekannt [Skottsberg s.n.] [HOLOTYPE: G (*non vidi*)]. First synonymised by Engel (1990*a*: 73).

Plants small, prostrate or procumbent, in loose, pale green, yellowish-green to brownish-green mats. *Stems* 3–5 cm long, pinnately to bipinnately lateral-intercalary branched, sometimes becoming microphyllous, flagelliform at the tips of branches. *Leaves* obliquely inserted, distant to rarely imbricate, sometimes slightly concave, asymmetric, quadrifid to 0.3–0.5 of the length, 0.3–0.4 mm long and 0.3–0.5 mm wide at base, mostly wider than long; lobes triangular, unequal, acute, 4–8 cells wide at base; dorsal margins convex from cordate base, entire or with 1–2

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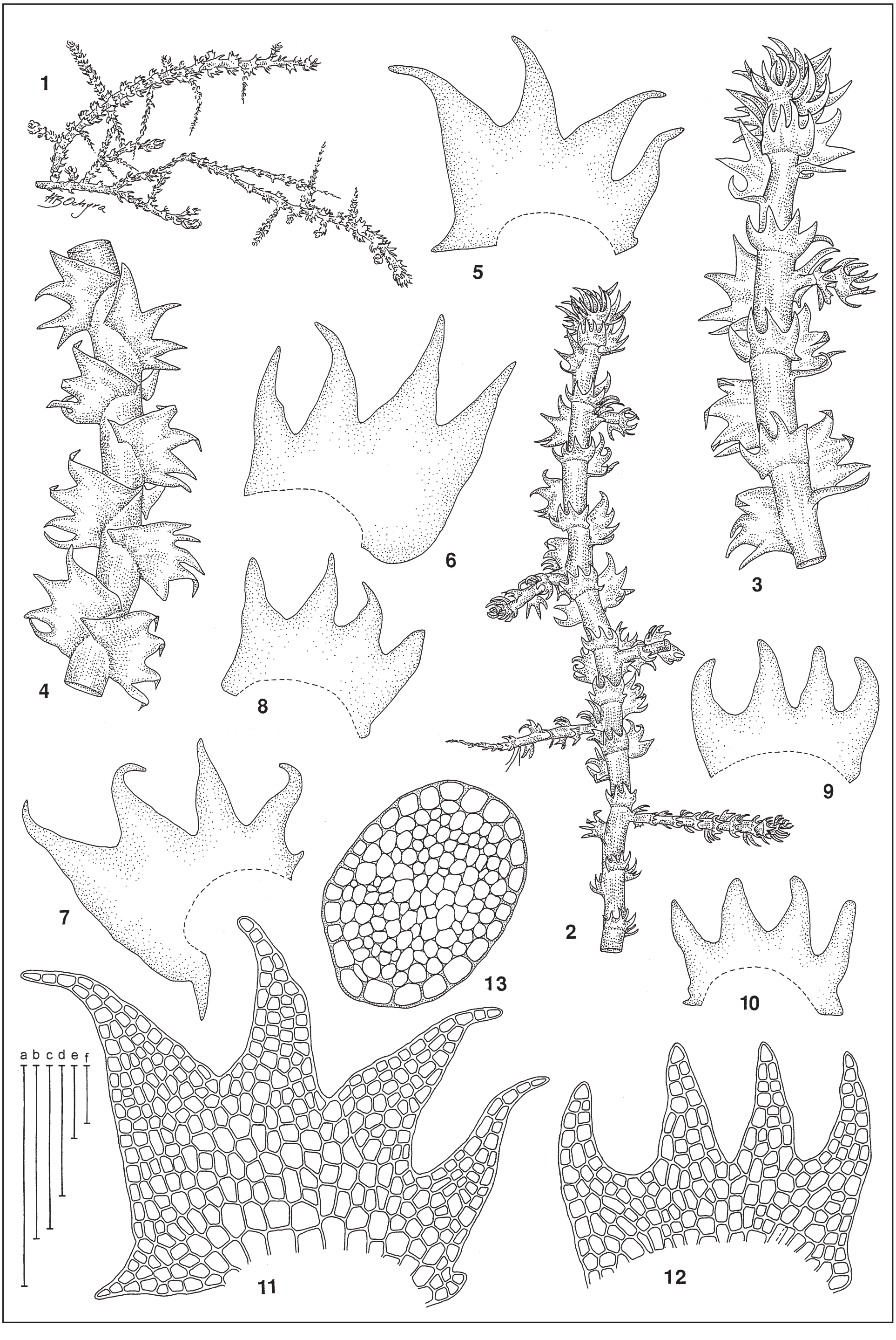
FIGURE 29. *Lepidozia chordulifera*. **1**. Habit of sterile plant. **2–3**. Shoots in ventral aspect. **4**. Shoot in dorsal aspect. **5–7**. Leaves. **8–10**. Underleaves. **11**. Leaf cells. **12**. Cells of amphigastrium. **13**. Transverse section of stem. (All from *Longton 635*, AAS.) Scale bars: a – 10 mm (1); b – 1 mm (8–10); c – 1 mm (5–7); d – 1 mm (3–4) and 100 µm (13); e – 1 mm (2); f – 100 µm (11–12).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teeth, ventral margins entire to toothed on well developed leaves; leaf cells ± quadrate, 10–20 × 18–25 µm, with thickened walls, without trigones, cuticle nearly smooth. *Underleaves* nearly as broad or slightly broader than the stem, similar to lateral leaves, quadrifid to 0.4–0.5 of the length, with the lobes 4–6 cells wide at base, entire or with 1 or occasionally more teeth on each side on well developed axes. *Remainder* unknown.

Taxonomic and nomenclatural notes. — *Lepidozia chordulifera* was described by Taylor (1846) from the specimens collected by C. Darwin in 1834 on Archipelago de los Chonos near Chiloe Island in the Valdivian Province in Chile. It was transferred to *Jungermannia* by Taylor and Hooker (1847) and to *Mastigophora* by Trevisan (1877) as *Jungermannia chordulifera* (Taylor) Hook. f. & Taylor and *Mastigophora chordulifera* (Taylor) Trevis., respectively, but these concepts have never gained wide acceptance. On the other hand, because of considerable plasticity, six phenotypes of *L. chordulifera* were recognised taxonomically as species in their own right, but Fulford (1966) and Engel (1990*a*) considered them to be merely ecological variants and reduced their names to synonymy. One of these names, *Lepidozia cuspidata* Steph., originally used for the plants from West Patagonia (Stephani, 1911), was adopted to describe material from the South Sandwich Islands by Grolle (1972*a*) and Longton and Holdgate (1979).

Differentiation. — The spinose basal margins of well developed leaves and underleaves are a characteristic feature of this species, separating it from all other species known from the southernmost part of South America.

Reproduction in Antarctica. — Fertile plants unknown.

Habitat. — In Antarctica known from wet soil near the shore of a lake in the South Sandwich Islands, and from moist *Chorisodontium aciphyllum* turf in the South Orkney Islands.

World range. — An American temperate species (Fig. 30, inset), widespread and rather abundant in the *Nothofagus* zone on the western fringes of southern South America, ranging from lat. *ca* 40°S in the Valdivian Province to Tierra del Fuego, the Falkland Islands and South Georgia and extending northwards to the Juan Fernandez Islands (Fulford, 1966; Engel, 1990*a*) and southwards to the northern maritime Antarctic. The report from Tasmania (Rodway, 1916) needs confirmation.

Distribution in Antarctica. — A rare species, collected from Candlemas Island in the South Sandwich Islands and from Signy Island in the South Orkneys where it occurs from near sea level to about 65 m (Fig. 31). It may be more widespread amongst *Chorisodontium aciphyllum* turf but is very easily overlooked.

Specimens examined. — SOUTH SANDWICH ISLANDS. CANDLEMAS ISLAND. Steaming lake on western shore, *ca* 35 m, *Longton 635* (AAS, KRAM).

SOUTH ORKNEY ISLANDS. CORONATION ISLAND. Cape Hansen, *ca* 50 m, *Lewis Smith 1852* (AAS, KRAM) and 85 m, *Lewis Smith 5231* (AAS, KRAM). SIGNY ISLAND. Borge Bay,

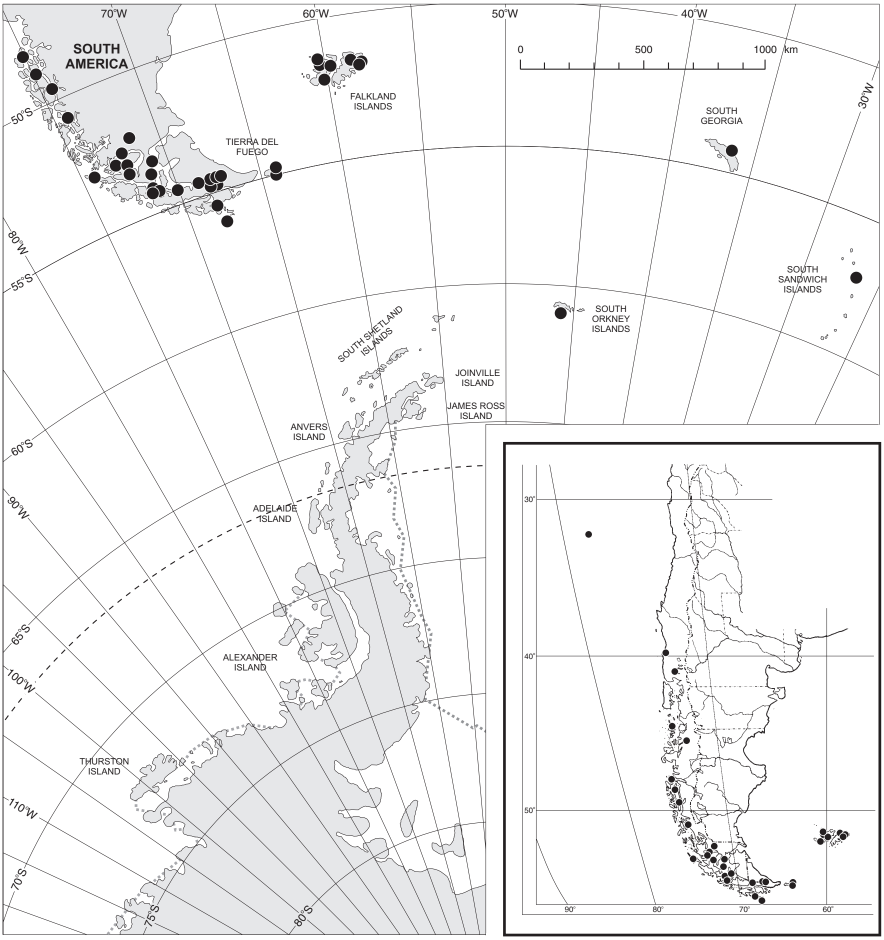

FIGURE 30. Distribution of *Lepidozia chordulifera* in the Antarctic and Fuegian region. Inset: distribution in South America.

Knife Point, *ca* 15 m, *Lewis Smith 10729 & 10933* (AAS, KRAM); Factory Cove, 50 m, *Lewis Smith 5203* (AAS, KRAM), *ca* 65 m, *Lewis Smith 303* (AAS, KRAM) and 80 m, *Lewis Smith 690* (AAS, KRAM); south-east shore of Factory Cove, 50 m, *Longton 1165* (AAS, KRAM); east side of Rusty Bluff above Paal Harbour, *ca* 30 m, *Lewis Smith 1839* (AAS, KRAM) and *ca* 35 m, *Lewis Smith 353B* (AAS, KRAM); above Paal Harbour, 75 m, *Lewis Smith 10865* (AAS, KRAM).

Literature records. — SOUTH SANDWICH ISLANDS: without indication of the island (Lewis Smith, 1993: 322 as *Lepidozia cuspidata*); Candlemas Island (Grolle, 1972*a*: 84; Longton and Holdgate, 1979: 10 as *Lepidozia cuspidata*; Ochyra & Váňa, 1989*b*: 215). SOUTH ORKNEY ISLANDS: Signy Island (Lewis Smith, 1972: 47; Ochyra & Váňa, 1989*b*: 215 both as *Lepidozia* sp.).

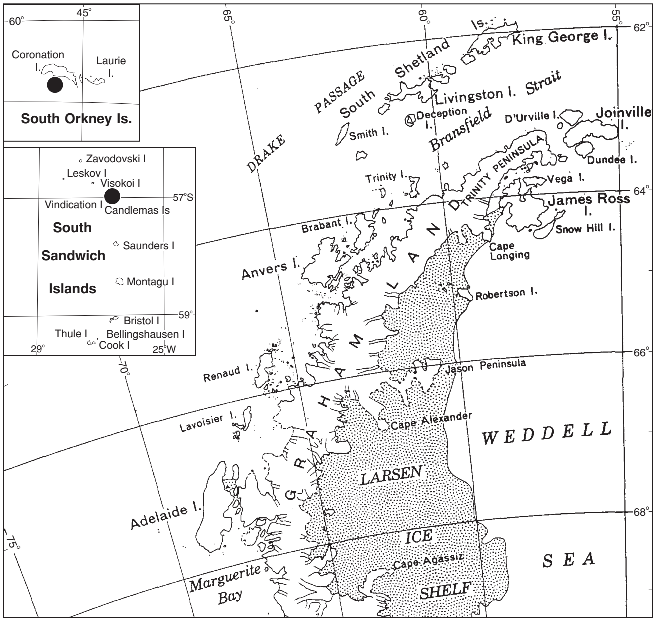

FIGURE 31. Distribution of *Lepidozia chordulifera* in the Antarctic.

Family III. CEPHALOZIACEAE MIG.

Cephaloziaceae Mig., Krypt.-Fl. Deutschl. **1**: 465. 1904. – TYPE: *Cephalozia* (Dumort.) Dumort.

Plants small to medium-sized, whitish-, yellowish- to brownish-green or mostly only green, rarely tinged with purple. *Stems* creeping to procumbent with occasionally ascending tips, simple or terminally (*Frullania*-type), rarely lateral-intercalary (*Plagiochila*-type, in some genera also *Anomoclada*-type) or ventral-intercalary (*Bazzania*-type) branched, in transverse section without or with a unistratose cortex forming a translucent hyalodermis. *Rhizoids* scattered on the ventral surface of the stem or on flagellae, hyaline to pale brown. *Leaves* succubous, obliquely to nearly transversely inserted, mostly bilobed, sometimes unlobed (in *Odontoschisma* and *Trabacellula*) or very rarely almost forming a thallus (in *Schiffneria*); leaf cells thin-walled, rarely slightly thick-walled, trigones mostly absent, occasionally present, nodulose (in *Odontoschisma*); cuticle smooth. *Underleaves* absent or represented by ephemeral stalked papillae, or small to well developed. *Asexual reproduction* sometimes present by 1–2-celled gemmae formed on the stem tips or leaf margins. *Dioecious* or *autoecious*, rarely *paroecious*. *Androecia* on short ventral-intercalary branches or on lateral branches; male bracts complicate-concave, bilobed, monandrous, with antheridia on biseriate stalks. *Gynoecia* on abbreviated ventral-intercalary branches; female bracts large, sometimes dentate to lobate-dentate. *Perianth* terete, 3–8-layered below, trigonous above, contracted at the mouth. *Seta* composed of 8(–9) rows of epidermal cells and 4(–5) rows of inner cells. *Capsule* ellipsoid, with 2–3-layered wall, outer wall with nodulose, inner wall with semilunate thickenings. *Spore* finely granulate-papillate; spore/elater width ratio 1–2 : 1.

The Cephaloziaceae are a medium-sized and very heterogeneous family comprising 14 genera subdivided into six subfamilies (Grolle, 1983*a*). It is difficult to circumscribe because of many apparent reticulate connections to several other families including the Lepidoziaceae, Antheliaceae, Adelanthaceae, Phycolepidoziaceae and Cephaloziellaceae (Schuster, 1964, 1974). However, characters such as the anatomical structure of the seta, which consists of 8(–9) epidermal and 4(–5) internal cell rows, always succubous, bilobed or unlobed leaves, ellipsoidal to obloid capsules with 2(–3)-stratose walls and monandrous male bracts, may serve as a good basis for the separation of the Cephaloziaceae. The family has a worldwide distribution and, in the context of the present Flora, it is represented by only one genus with a single species.

1. **CEPHALOZIA** (DUMORT.) DUMORT.

Cephalozia (Dumort.) Dumort., Recueil Observ. Jung.: 18. 1835. – *Jungermannia* L. sect. *Cephalozia* Dumort., Sylloge Jung. Eur. Indig.: 60. 1831. – LECTOTYPE: *Cephalozia bicuspidata* (L.) Dumort. (*Jungermannia bicuspidata* L.) (*fide* Bonner, 1963: 536).

Plants small to medium-sized, mostly green, but also yellowish-, brownish- to whitish-green, rarely with purplish pigmentation. *Stems* soft-textured, prostrate to creeping, with terminal or ventral-intercalary branches, in transverse section with a hyalodermis of 10–12 rows of large cells, surrounding smaller medullary cells with thickened and pitted walls. *Leaves* remote to contiguous, rarely imbricate, succubously to subtransversely inserted, patent to erecto-patent, slightly to strongly decurrent, bilobed or exceptionally unlobed, with entire margins; lobes acute to subacute, often connivent; sinus descending to 0.2–0.8 of the leaf length; leaf cells mostly thin-walled, rarely slightly thick-walled, without trigones; cuticle smooth or nearly so. *Underleaves* absent. *Gemmae* rarely produced on the shoot tips. *Dioecious* or *autoecious*, very rarely *paroecious* to *heteroecious*. *Male inflorescence* on the main shoots or on short ventral-intercalary branches; male bracts with basal tooth, monandrous. *Female inflorescences* on short ventral-intercalary branches; female bracts larger than the leaves, deeper bilobed, often lobate or dentate. *Perianth* fusiform, bluntly trigonous. *Seta* composed of 8 rows of epidermal and 4 rows of internal cells. *Capsule* ellipsoidal to ovoid, with a bistratose wall.

Cephalozia is the largest genus in the Cephaloziaceae having a subcosmopolitan distribution, although most of its species occur in the Northern Hemisphere. Schuster (1974) estimated the total number of species of this genus to be 30–40 but Váňa (1988), in his synopsis of *Cephalozia*, recognised only 24–25 species, with the reservation that the status of some taxa still needs to be clarified. He subdivided the genus into three subgenera, of which the type subgenus is the most primitive, taxonomically most difficult and with 20 species it is the largest subgenus of *Cephalozia*. The remaining two, subgen. *Macrocephalozia* R. M. Schust. and subgen. *Eocephalozia* R. M. Schust., are small taxa each consisting of two species. The latter subgenus is restricted in its distribution to southern South America and one species, *C. badia*, extends to Antarctica.

1. ***Cephalozia badia*** (GOTTSCHE) STEPH. FIG. 32

Cephalozia badia (Gottsche) Steph., Bull. Herb. Boissier Sér. 2, **8**(7): 483. 1908 (X) [= Sp. Hepat. **3**: 313. 1908 (XI)]. – *Jungermannia badia* Gottsche *in* Neumayer, Deutsch. Exp. Int. Polarforsch. **2**: 452. 1890.

– *Lophozia badia* (Gottsche) Steph., Wiss. Erg. Schwed. Südpol. Exp. 1901–1903, **4**(1): 8. 1905. – TYPE: Dr Will Nr. 37. Süd-Georgien. Köppenberg 10. Februar 1883 [HOLOTYPE: "Herbarium Regnum Monacense. Cephalozia badia (Gottsche) Süd-Georgien. Köppenberg. 10.II.1883. leg. Will" – M!].

Cephalozia cucullifolia Steph., Wiss. Ergebn. Schwed. Südpolar-Exp. 1901–1903 **4**(1): 2. 1905. – TYPE: Antarktis: Südshetlandsinseln, Nelsoninsel, Harmony Cove in der Polytrichummatte, 11/I 1902 [HOLOTYPE: G-13202!]. First synonymised by Grolle (1972*a*).

Cephalozia badia (Gottsche) Steph. fo. *minor* Grolle, Br. Antarct. Surv. Bull. **28**: 83. 1972, *nom. nud.* – ORIGINAL MATERIAL: South Sandwich Islands, Leskov Island, summit ridge, *Longton 501* – AAS!, KRAM!; Candlemas Island, western shore, *Longton 634* – AAS!, KRAM!, ***syn. nov.***

Plants small, slender, soft, prostrate, procumbent or ascending, in thin, loose to compact mats or erect in moss cushions, whitish-green, green to mostly brownish above. *Stems* 1.0–1.5 cm long, mostly with terminal or with small-leaved ventral-intercalary branches, in transverse section consisting of 13–15 rows of thin-walled cortical cells surrounding only slightly smaller medullary cells. *Rhizoids* rare, scattered, arising from the ventral part of the stem, hyaline or brownish. *Leaves* succubously to subtransversely oriented, distant to contiguous, irregularly spreading with the lobes usually incurved, concave to cucullate, widely ovate in outline, bilobed to 0.3–0.4 of the length; lobes broadly triangular, acute to subacute, 6–8(–10) cells wide at base, with entire margins; leaf cells quadrate, subquadrate to rectangular, with slightly evenly thickened and mostly brownish-coloured cell walls, 25–30 µm wide; cuticle slightly verruculose. *Underleaves* absent. *Dioecious* (or *autoecious*?). *Androecia* not found. *Gynoecia* terminal; female bracts larger than the vegetative leaves, divided into some lobes, slightly dentate. *Perianth* long exserted, fusiform, plicate and slightly trigonous above, with the crenulate mouth. *Capsule* ovoid-cylindrical, nearly 1 mm long, with the bistratose wall; outer wall with nodulose thickenings on the radial walls; inner wall with semilunate thickenings. *Spores* papillose, 11–14 µm in diameter; elaters bispiral; spore/elater width ratio 2 : 1.

Taxonomic and nomenclatural notes. — The species was originally described as *Jungermannia badia* by Gottsche (1890) from material collected on South Georgia during the German International Polar-Year Expedition of 1882–1883. It was subsequently transferred to *Lophozia* (Stephani, 1905) and later the same author moved it correctly to *Cephalozia* (Stephani, 1908). In 1902 C. Skottsberg collected this species on Nelson Island in the South Shetland Islands during the Swedish South Polar Expedition of 1901–1903 and this material was originally described by Stephani (1905) as a separate species, *Cephalozia cucullifolia*. Because the type material of this species fits well the South Georgian type of *C. badia*, Grolle (1972*a*) reduced both names to synonymy, the latter having priority.

The Antarctic plants of *Cephalozia badia* show a considerable plasticity with regard to size. Grolle (1972*a*) suggested the recognition of some small plants from the South Sandwich Islands as fo. *minor* Grolle, but he failed to provide the Latin

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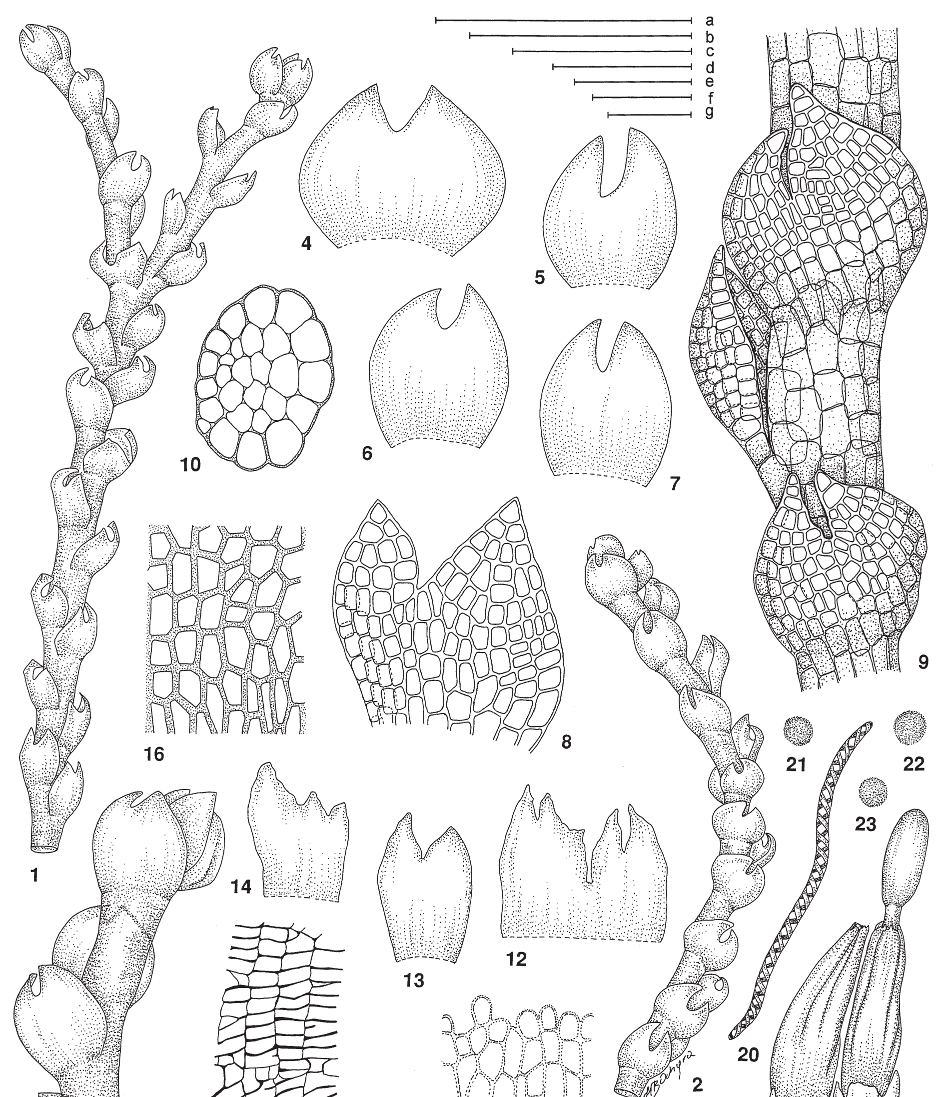
FIGURE 32. *Cephalozia badia*. **1–3**. Sterile plants. **4–7**. Leaves. **8**. Leaf cells. **9**. Leaves and portion of stem. **10**. Transverse section of stem. **11**. Perianth-bearing shoot. **12–14**. Bracts. **15**. Portion of perianth mouth. **16**. Perianth cells in middle part. **17**. Sporophyte. **18**. Epidermal cells of capsule wall. **19**. Inner cells of capsule wall. **20**. Elater. **21–26**. Spores. (1–10 from *Ochyra 2187/80*; 11–26 from *Convey 153*; all in KRAM.) Scale bars: a – 0.5 mm (4–7) and 100 µm (15–16); b – 1 mm (1–2) and 0.5 mm (3); c – 1 mm (12–14, 17); d – 100 µm (18–19); e – 1 mm (11); f – 100 µm (8, 10) and 50 µm (20–26); g – 100 µm (9).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diagnosis of it, thus invalidly publishing this name. Apart from the smaller stature these plants exhibit all features of the otherwise typical plants of this species. Therefore, they are interpreted to be merely ecotypes of this species which develop in the harsh climatic conditions which do not deserve taxonomic recognition. Accordingly, fo. *minor* is reduced to synonymy of *C. badia*.

Differentiation. — *Cephalozia badia* is the only representative of the genus in Antarctica. It can be confused with *Cephaloziella varians* from which it differs in its larger cells and concave leaves. The species is closely related to *C. heteroica* J. J. Engel decribed recently from the Brunswick Peninsula in southern South America (Engel, 1978). This species differs from *C. badia* in having occasionally trilobed leaves, the stem consisting of only 11–12 rows of cortical cells and its paroecious to heteroecious inflorescences. Unfortunately, *C. badia* is known only as female plants or in sterile condition. Whether both species are significantly different can be deduced only when well-developed fertile plants of *C. badia* are discovered. *Clasmatocolea rigens* is the only other species in Antarctica with bilobed leaves but it can be separated from *C. badia* by the presence of underleaves.

Reproduction in Antarctica. — Mostly sterile, but three populations have been recorded with mature sporophytes.

Habitat. — On moist to wet soil at the margin of melt water channels, on moist rock ledges, usually intermixed with turf-forming mosses such as *Pohlia nutans*, *Polytrichastrum alpinum* and *Polytrichum piliferum*.

World range. — An American subantarctic species known from South Georgia from where it was described (Gottsche, 1890), and the maritime Antarctic from the South Sandwich Islands to the Argentine Islands off the Graham Coast (Fig. 33). In South America *Cephalozia badia* is rare in Tierra del Fuego (Fulford, 1968) and in Western Patagonia (Hässel de Menendez & Solari, 1985) and, additionally, it is scattered on the Falkland Islands (Engel, 1990*a*). Because all these localities are situated at higher elevations, the species is interpreted as sub-Antarctic rather than south-cool temperate.

Distribution in Antarctica. — The species is widely distributed, though infrequent, on the South Sandwich Islands, South Orkney Islands, South Shetland Islands and on the west Antarctic Peninsula extending from the Davis Coast to the Argentine Islands off the Graham Coast at lat. 65°15'S (Fig. 34).

Specimens examined. — SOUTH SANDWICH ISLANDS. LESKOV ISLAND. Summit ridge, *ca* 200 m, *Longton 501 & 515A* (AAS, KRAM). CANDLEMAS ISLAND. Lucifer Hill, north-west ridge active fissure, *Convey 220D* (AAS, KRAM); Clinker Gulch, *Convey 151D, 153 & 163C* (AAS, KRAM); west shore, *Longton 634* (AAS, KRAM); north of western lagoon, *Longton 708* (AAS, KRAM, M), *709A & 710* (AAS, KRAM); north of eastern lagoon, *Longton 785* (AAS, KRAM).

SOUTH ORKNEY ISLANDS. LYNCH ISLAND. Without specific locality, *ca* 15 m, *Lewis*

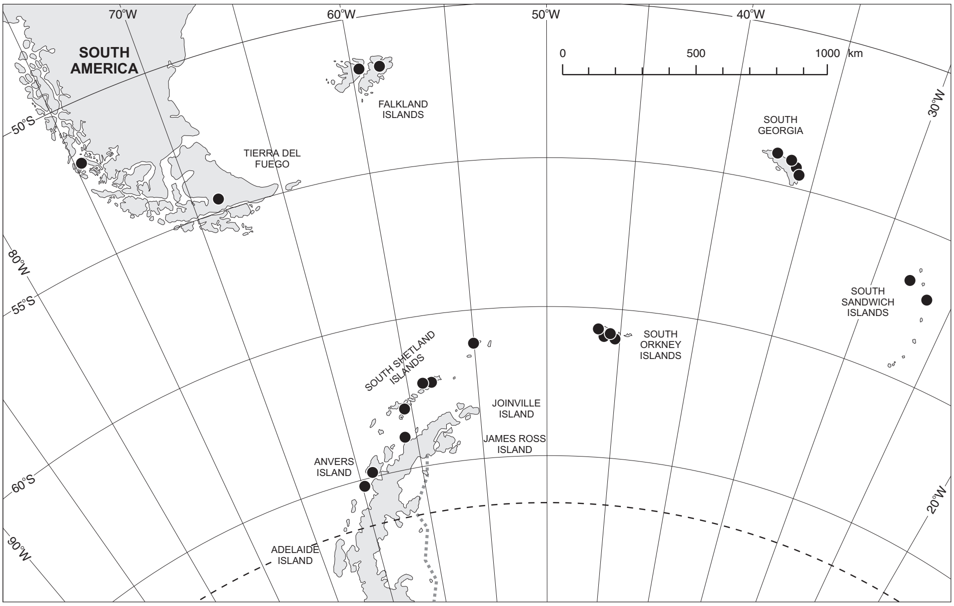


FIGURE 33. Global distribution of *Cephalozia badia*.

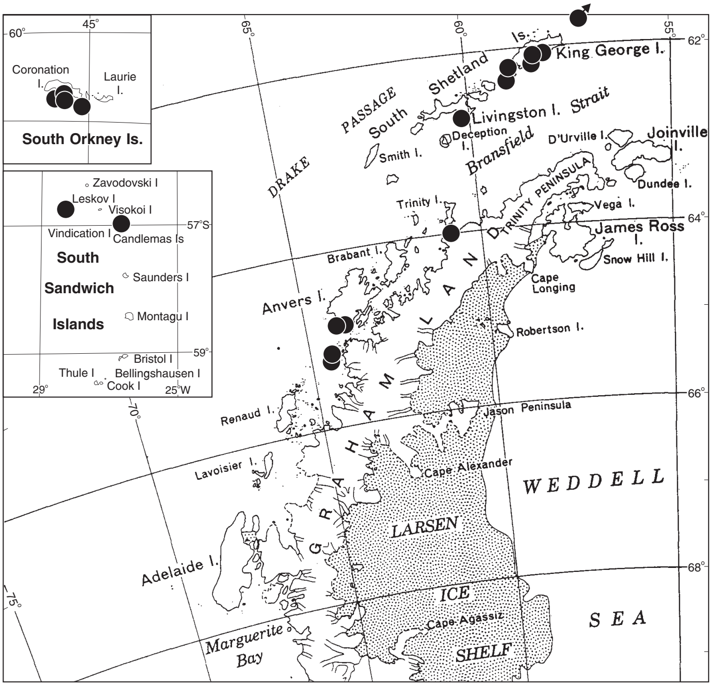


FIGURE 34. Distribution of *Cephalozia badia* in the Antarctic. The locality on Elephant Island is indicated by an arrow.

Smith 530 (AAS, KRAM). MATTHEWS ISLAND. Promontory north of Coffer Island, *ca* 35 m, *Lewis Smith 191B* (AAS, KRAM). SIGNY ISLAND. North-east of Express Cove, *ca* 50 m, *Lewis Smith 618* (AAS, KRAM); coast opposite Spindrift Rocks, *ca* 65 m, *Longton 1146* (AAS, KRAM); north-west coast, 50 m, *Lewis Smith 479B* (AAS, KRAM); Factory Cove, above the station, 75 m, *Lewis Smith 5201B* (AAS); between Factory Cove and Paal Harbour, *ca* 15 m, *Holdgate 135B* (AAS, KRAM); east side of Rusty Bluff above Paal Harbour, *ca* 85 m, *Lewis Smith 425A* (AAS, KRAM); between Observation Bluff and Polynesia Point, *ca* 15 m, *Longton 1082* (AAS, KRAM); Moraine Valley, 30 m, *Lewis Smith 5206B* (AAS) and 65 m, *Lewis Smith 5205D* (AAS, KRAM) and 100 m, *Lewis Smith 317B* (AAS, KRAM); west side of Rusty Bluff in Moraine Valley, 50 m, *Lewis Smith 551B* (AAS, KRAM); Gourlay Peninsula, *ca* 35 m, *Lewis Smith 358* (AAS, KRAM). MOE ISLAND. Alt. 30–200 m, *Lewis Smith 5240C* (AAS, KRAM).

SOUTH SHETLAND ISLANDS. ELEPHANT ISLAND. 2 km south-west of Endurance Glacier, 152 m, *Allison 28B* (AAS). KING GEORGE ISLAND. ***Admiralty Bay***: Italia Valley, 100 m, *Ochyra 89/80 & 91/80* (KRAM, PRC); Ore Point, 4 m, *Ochyra 515/80* (KRAM, PRC); Mt. Wawel, 30 m, *Ochyra 2187/80* (KRAM, PRC). ***Fildes Peninsula***: Ardley Island, 10 m, *Ochyra 2491/80* (KRAM, PRC) and *Nikolaev 2 & 8* (LE, PRC). NELSON ISLAND. Harmony Cove, *Skottsberg 400* (G – type of *Cephalozia cucullifolia*). LIVINGSTON ISLAND. False Bay, *Schmitt 221B* (KRAM, NY).

WEST ANTARCTIC PENINSULA. DAVIS COAST. Cape Andreas, 29 Nov 1902, *Skottsberg s.n.* (G). DANCO COAST. ***Anvers Island***: Norsel Point, *Komárková 63* (KRAM); Litchfield Island, *Komárková 86A* (KRAM). GRAHAM COAST. ***Argentine Islands***: Galindez Island, 2 m, *Lewis Smith 754* (AAS, KRAM); north-west corner of Galindez Island, *ca* 15 m, *Longton 1255* (AAS, KRAM); Galindez Island, Meek Channel, *ca* 35 m, *Longton 1333* (AAS, KRAM); Corner Islands, *ca* 35 m, *Longton 1342* (AAS, KRAM).

Literature records. — SOUTH SANDWICH ISLANDS. Leskov and Candlemas Islands (Grolle, 1972*a*: 83; Longton & Holdgate, 1979: 10; Ochyra & Váňa, 1989*b*: 215). SOUTH ORKNEY ISLANDS. Signy and Coronation Islands (Ochyra & Váňa, 1989*b*: 215); without indication of the island (Fulford, 1968: 326). SOUTH SHETLAND ISLANDS. Elephant Island (Allison & Lewis Smith, 1973: 187; Lewis Smith, 1979*a*: 235; Ochyra & Váňa, 1989*b*: 215); King George Island (Ochyra & Váňa, 1989*a*: 195, 1989*b*: 215; Myrcha *et al.*, 1991: 163); Nelson Island (Stephani 1905: 4; Skottsberg, 1912: 6; Steere, 1961: 30; Corte, 1962: 7; Fulford, 1968: 326 all as *Cephalozia cucullifolia*; Grolle, 1972*a*: 86; Ochyra & Váňa, 1989*b*: 215). WEST ANTARCTIC PENINSULA. Davis Coast: Cape Andreas (Skottsberg, 1912: 8 as *Lophozia badia*); Danco Coast: Orléans Strait (Stephani, 1905: 8; Steere 1961: 30; Corte, 1962: 7 both as *Lophozia badia*; Ochyra & Váňa, 1989*b*: 215).

CEPHALOZIACEAE SPECIES EXCLUDED FROM ANTARCTICA

Cephalozia bicuspidata (L.) Dumort. — This species was reported from Fildes Peninsula on King George Island, South Shetland Islands, by Chen *et al.* (1993, 1995) but the voucher specimen (*Li 930328*, AAS) is *Pachyglossa dissitifolia*.

Odontoschisma macounii (Austin) Underw. — This species was reported from Fildes Peninsula on King George Island, South Shetland Islands, by Chen *et al.* (1993, 1995) and was the first record of this species in the Southern Hemisphere. However, it is based on misidentification and the voucher specimen (*Li 930327*, AAS) is, in fact, *Herzogobryum teres*. Accordingly, *Odontoschisma macounii* has to be excuded from the hepatic flora of Antarctica and it still retains the status of a Holarctic species which has never been correctly reported in the Southern Hemisphere.

Family **IV. CEPHALOZIELLACEAE** DOUIN

Cephaloziellaceae Douin, Mém. Bull. Soc. Bot. France **29**: 1, 5, 13. 1920. – TYPE: *Cephaloziella* (Spruce) Schiffn.

Plants very small to minute, green, brownish to reddish. *Stems* prostrate or ascending, simple or ventral-intercalary (*Bazzania*-type), lateral-intercalary (*Plagiochila*-type) or rarely also terminally (*Frullania*-type, exceptionally also *Acromastigium*-type) branched, mostly without flagellae or stolons, in transverse section with a slightly differentiated or undifferentiated cortex. *Rhizoids* scattered on the ventral side of the stem, usually hyaline. *Leaves* succubous to subtransversely or transversely inserted, remote or contiguous, mostly bilobed to deeply bifid (unlobed in some species of *Kymatocalyx*), with entire or dentate margins; leaf cells small, mostly thick-walled, without or with only minute trigones; cuticle smooth to coarsely papillose. *Underleaves* present, well developed to very small, or absent. *Gemmae* usually present on modified or unmodified leafy shoots. *Dioecious*, *paroecious* or *autoecious*, sometimes also *heteroecious*. *Androecia* becoming intercalary on the main stem or lateral branches; male bracts saccate, slightly larger than the leaves, monandrous, with a uniseriate antheridial stalk. *Gynoecia* on elongate or short axes, terminal; female bracts similar to the leaves or more dentate; bracteoles present, sometimes connate with bracts. *Perianth* 3–5-plicate, polystratose at base, little contracted to the rather wide mouth. *Perigynium* absent. *Seta* normally with 4 large epidermal opposed to 4 much smaller inner cells, occasionally with seta of the 8 + 4 or 10–12 + 8 type. *Capsule* ovoid to ellipsoidal, with 2(–3)-stratose wall; outer wall with nodular thickenings mostly on longitudinal walls; inner wall with nodular or incomplete semiannular thickenings. *Spores* finely papillose to verruculose, very small, 6–13 µm in diameter; elaters free, bispiral, hardly tortuous; spore/elater width ratio 1.5–2 : 1.

The Cephaloziellaceae are not easy to circumscribe and many of its members are externally similar to those of the Cephaloziaceae. Because of the scarcity of useful gametophytic criteria which, additionally, are often difficult to perceive, the family is mostly characterised by a suite of sporophytic characters (Schuster, 1971, 1980*a*, 1996*a*). Of these, the most useful is the anatomical structure of the seta which exhibits the classic 4 + 4-seriate pattern compared to the 8 + 4 seta anatomy in the Cephaloziaceae, although some exceptions from this pattern are known. The Cephaloziellaceae are a medium-sized, subcosmopolitan family which avoid only arid regions. Grolle (1983*a*) placed in it one large and six rather small genera. Later Schuster (1995*b*) added to the family the monotypic Australasian genus *Cephalomitrion* R. M. Schust. and Grolle (1995) transferred to it the genus *Stenor-*

rhipis Herzog. Because most of these small genera are restricted to the cool temperate areas of the Southern Hemisphere, Schuster (1980*a*, 1995*b*) postulates that the Cephaloziellaceae are probably Gondwanalandic in origin. In Antarctica the family is represented by a single genus and two species.

1. CEPHALOZIELLA (SPRUCE) SCHIFFN.

Cephaloziella (Spruce) Schiffn. *in* Engl. & Prantl, Nat. Pflanzenfam. **1**(3): 98. 1893, *nom. cons.* – *Cephalozia* (Dumort.) Dumort. sect. *Cephaloziella* Spruce, On Cephalozia: 23, 62. 1882. – TYPE (*cons.*): *Cephaloziella divaricata* (Sm.) Schiffn. (*Jungermannia divaricata* Sm.).

Lepidoziella Mahu, Bol. Antárt. Chileno **7**: 3. 1987, *nom. inval.*, ***syn. nov.***

Plants very delicate, in loose or dense mats, sometimes in short tufts, green or brownish, rarely reddish or blackish. *Stems* prostrate or creeping, often erect among taller plants, only a few millimetres long, simple or mostly lateral-intercalary to ventral-intercalary branched, with an ill-defined cortex. *Leaves* transversely to succubously oriented, mostly distant but occasionally imbricate, bilobed to 0.5–0.8 their length, smooth or with scattered conical projections on the dorsal surface; lobes ovate- or lanceolate-triangular, sometimes oblong, with entire to dentate margins, subequal to equal; leaf cells mostly with thickened walls. *Underleaves* variable in shape from spiniform to triangular or ovate to filiform or subulate, often bidentate or bifid, sometimes absent. *Gemmae* present in some species on leaves and underleaves on ascending shoots, ovoid to angulate, 2-celled. *Dioecious* or *monoecious*. *Androecia* spicate; male bracts monandrous, erect to suberect in 3–10(–15) pairs. *Gynoecia* terminal; female bracts similar to the leaves; bracteoles 2–3-lobed, with ovate- or sometimes lanceolate-triangular lobes. *Perianth* trigonous to 4-plicate, with a wide, mostly crenulate mouth. *Seta* with 4 large epidermal and 4 small internal cells. *Capsule* ovoid to ellipsoid, with bistratose wall. *Spores* very small, smooth to finely verruculose; elaters free, bispiral; spore/elater width ratio mostly 1 : 1.

Cephaloziella is the largest genus in the Cephaloziellaceae having a worldwide distribution. It is poorly known taxonomically and is one of the most difficult of all genera among the liverworts. There are about 90 species validly described in *Cephaloziella*. Many of these were recognised by Douin (1914*a*, *b*, 1916, 1920, 1927, 1928) in his detailed study of this genus. Unfortunately, he introduced serious confusion with regard to the taxonomy of this genus, mainly because he presented an uncritical concept of species, often recognised on the basis of the sterile material. Many species of *Cephaloziella* are notoriously variable; variations are often strictly environmental, resulting in numerous phenotypes which were given taxonomic status. The phenotypic variation is coupled with the high reduction and morphological simplification of the plants, resulting in a paucity of characters useful in separating species. Consequently, the species can usually be determined by the presence or absence of underleaves in sterile stems and the sex of plants. The sporophyte characters are seldom available in plants growing in harsh polar conditions, and therefore their correct determination is very difficult or impossible.

There have been many recent regional studies devoted to *Cephaloziella*, but a worldwide revision of this genus is still awaited. Some species from the sub-Antarctic and New Zealand were investigated by Schuster (1971, 1996*a*). The Latin

American taxa were monographed by Fulford (1976) but her treatment is neither very critical nor complete, and consequently of limited value.

Cephaloziella is subdivided into five subgenera and several sections (Schuster, 1980*a*, 1996*a*). Two species of the genus are known from the Antarctic and one of them is the most frequent and abundant of all hepatic species in this region. They represent the type subgenus but belong within two different sections, sect. *Byssaceae* R. M. Schust. (*C. hispidissima*) and sect. *Rubellae* R. M. Schust. (*C. varians*). The two regional species may be recognised in the following key.

KEY TO THE ANTARCTIC SPECIES OF *CEPHALOZIELLA*

1. Stems and the dorsal leaf surface spinose .... **1. *C. hispidissima***
1. Stems and the dorsal leaf surface smooth .... **2. *C. varians***

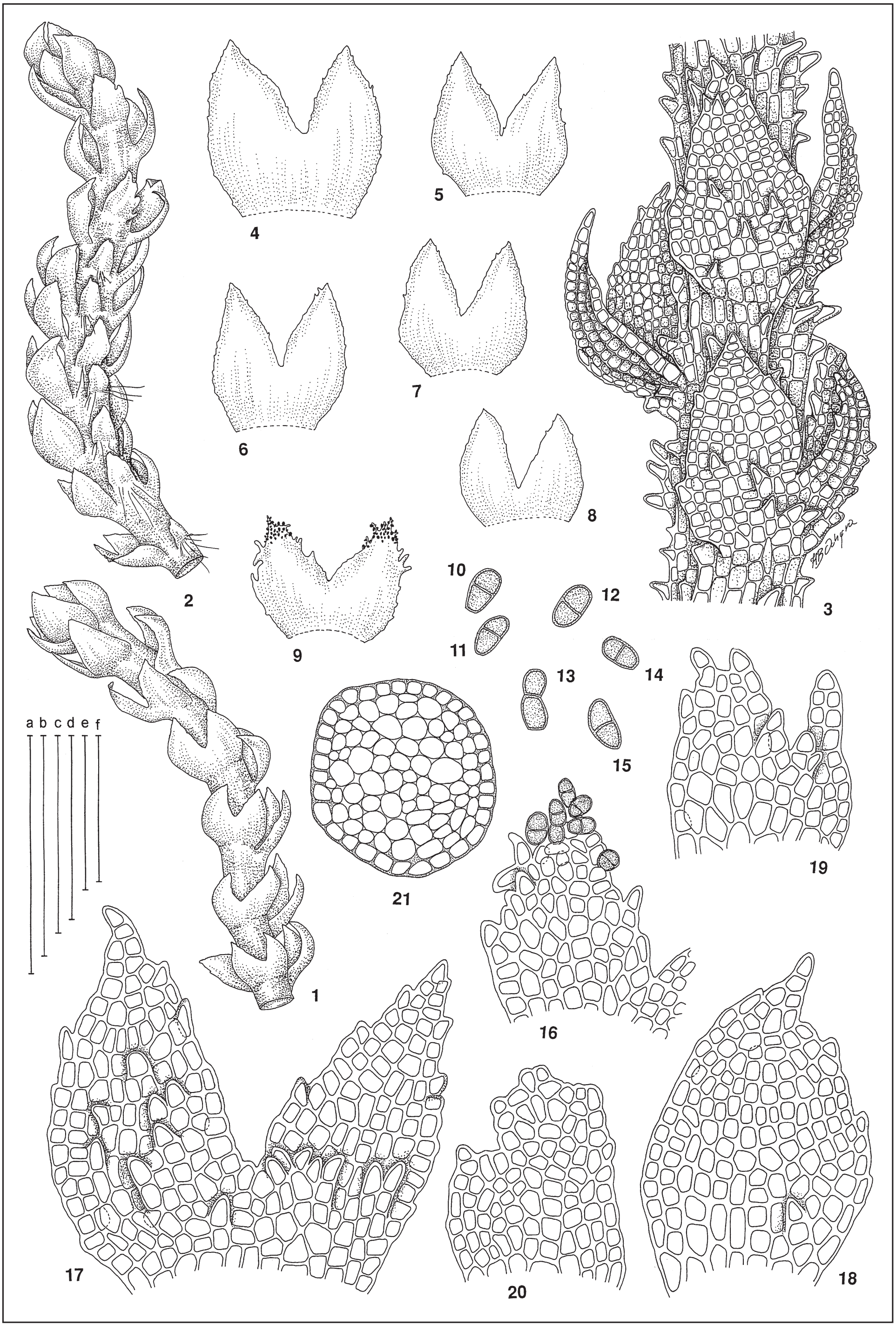
1. ***Cephaloziella hispidissima*** R. M. SCHUST. FIG. 35

Cephaloziella hispidissima R. M. Schust., Nova Hedwigia **22**: 208, *p. 23, f. 1–9.* 1973 [*C. hispidissima* R. M. Schust., Antarct. Journ. U.S. **4**(4): 103. 1969, *nom. nud.*]. – TYPE: Argentina, Tierra del Fuego, Cerro Garibaldi, SE. of Lago Escondido, near Rte 3 between Ushuaia and Rio Grande, *ca* 950 m, in alpine zone of rather dry cliff face, in crevices with *Distichium capillaceum*, *RMS 58304* [HOLOTYPE: Hb. R. M. Schuster (*non vidi*)].

Plants minute, scattered or in small patches, dull, green to brownish. *Stems* only a few millimetres long, creeping to ascending with leafy shoots only 0.4–0.5 mm wide, rather rigid and wiry in texture, simple or irregularly branched with axillary, intercalary branches, hispid on its surface by 1–2-celled projections, 30–40 µm long, terminated by elongate cells, 20–30 µm long, in transverse section 10–12 cells wide, consisting of an undifferentiated cortex. *Rhizoids* scattered on the ventral side of the stem, relatively rare. *Leaves* contiguous to subcontiguous, large, 0.16–0.21 mm long, 0.18–0.23 mm wide, transversely inserted, slightly conduplicate, bilobed to 0.6–0.8 their length; lobes triangular, acute to apiculate, 8–12(–14) cells wide at base, with entire to paucidentate margins, with sharp spiniform projections on the dorsal face. *Leaf cells* thick-walled, 15–20 × 10–13 µm, with thickened walls and without trigones. *Underleaves* rather large, mostly bifid, lobate or dentate. *Gemmae* ovate, smooth, bicellular, 18.5–26.5 µm long, 9–11 µm wide, formed on the lobe margins on some apical leaves. *Gametangia* and *sporophytes* unknown in Antarctica.

Taxonomic and nomenclatural notes. — The species was described from Paso Garibaldi on Isla Grande de Tierra del Fuego (Schuster, 1971). It clearly belongs within sect. *Byssaceae* on the basis of its leaf form and large underleaves and it seems to be a close relative of the Appalachian-Japanese *Cephaloziella spinicaulis* Douin. *C. hispidissima* was first reported as a new species by Schuster (1969*a*) from material collected on Livingston Island in the Antarctic. However, he (Schuster, 1971) failed to include this material in the protologue and based his description on the plants from Tierra del Fuego and New Zealand.

Differentiation. — The species is very distinctive in its spinose stems and dentate leaves which have sharp projections on the dorsal surface, as well as large



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underleaves. These features make it unlikely to be confused with any other liverwort species in the Antarctic.

Reproduction in Antarctica. — Fertile plants unknown, but some populations produce abundant bicellular gemmae which have not previously been described in this species.

Habitat. — *Cephaloziella hispidissima* occurs in rather dry situations on soil on rock ledges or, more frequently, over the moribund surface of the moss turves and cushions, e.g. *Andreaea depressinervis*, *A. gainii*, *Pohlia nutans* and *Polytrichastrum alpinum*; also amongst shoots of *Chorisodontium aciphyllum* in exposed and dry parts of deep moss banks overgrown with lichens. Also on fine mineral fellfield soil cultured *in situ* beneath experimental cloches on Signy Island (Factory Bluffs).

World range. — A rare and infrequent species known from Otago Province on South Island, New Zealand, and Tierra del Fuego, and extending to the northern maritime Antarctic (Fig. 36). Ochyra and Váňa (1989*b*) considered *Cephaloziella hispidissima* to be an amphipacific south-temperate species. Because it seems to have its main centre of distribution in Antarctica and its more northerly stations are at high elevations (*ca* 950 m in Tierra del Fuego and *ca* 1700 m in New Zealand), *C. hispidissima* should be considered as a subantarctic rather than cool south-temperate species.

Distribution in Antarctica. — A rare species known only from the South Orkney and South Shetland Islands, extending to lat. *ca* 63°S on Deception Island (Fig. 37).

Specimens examined. — SOUTH ORKNEY ISLANDS. **SIGNY ISLAND**. Observation Bluff, 50 m, *Lewis Smith 402B* (AAS, KRAM); above Paal Harbour, *ca* 85 m, *Lewis Smith 670A* (AAS, KRAM); Factory Bluffs, 120 m, *Lewis Smith 8698* (AAS, KRAM) and without elevation, *Lewis Smith 10891C* (AAS, KRAM).

SOUTH SHETLAND ISLANDS. **KING GEORGE ISLAND**. ***Admiralty Bay***: Demay Point, 40 m, *Ochyra 1370/80* (KRAM, PRC); Jersak Hills, 100 m, *Ochyra 5069A/79* (KRAM, PRC). ***Fildes Peninsula***: Ardley Island, 10 m, *Ochyra 2487/80* (KRAM, PRC). **AITCHO ISLAND**. Without detailed locality data, 7 Feb 2000, *Kuc s.n.* (Hb. Kuc). **HALF MOON ISLAND**. Without detailed locality data, 8 Feb 2000, *Kuc s.n.* (Hb. Kuc). **LIVINGSTON ISLAND**. ***Hurd Peninsula***: South Bay, 50 m, *Schulz 188* (Hb. Schulz, KRAM). **DECEPTION ISLAND**. Without closer locality data, 9 Feb 2000, *Kuc s.n.* (Hb. Kuc).

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FIGURE 35. *Cephaloziella hispidissima*. **1–2**. Sterile plants. **3**. Leaves and portion of stem. **4–8**. Leaves. **9**. Gemmae-bearing leaf. **10–15**. Gemmae. **16**. Gemmiferous leaf lobe. **17**. Leaf cells. **18–20**. Underleaves. **21**. Transverse section of stem. (1–9, 18–20 from *Ochyra 1370/80*; 10–17, 21 from *Ochyra 5069A/79*; all in KRAM.) Scale bars: a – 100 µm (10–15); b – 0.5 mm (1–2); c – 100 µm (17); d – 100 µm (16, 18–20); e – 100 µm (21) and 200 µm (4–9); g – 100 µm (3).

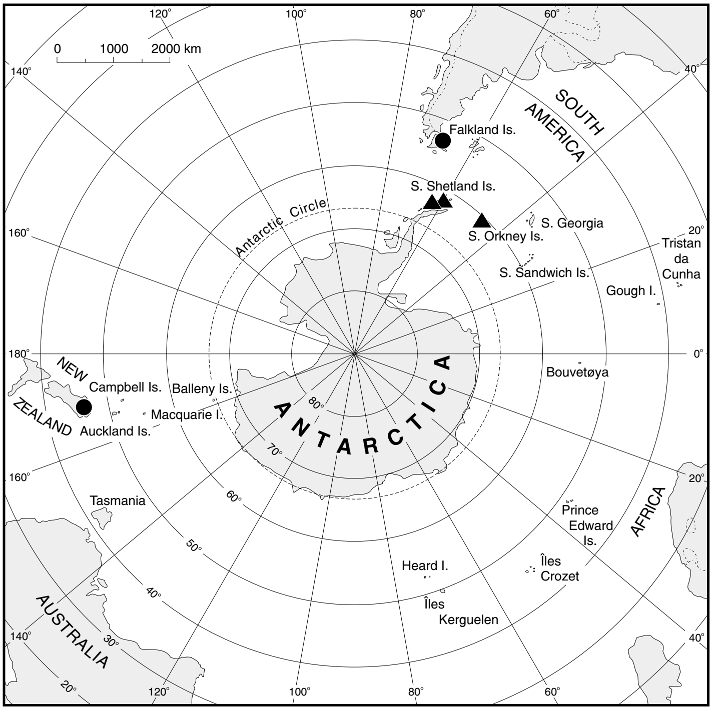

FIGURE 36. Global distribution of *Cephaloziella hispidissima*. The Antarctic localities are indicated by triangles.

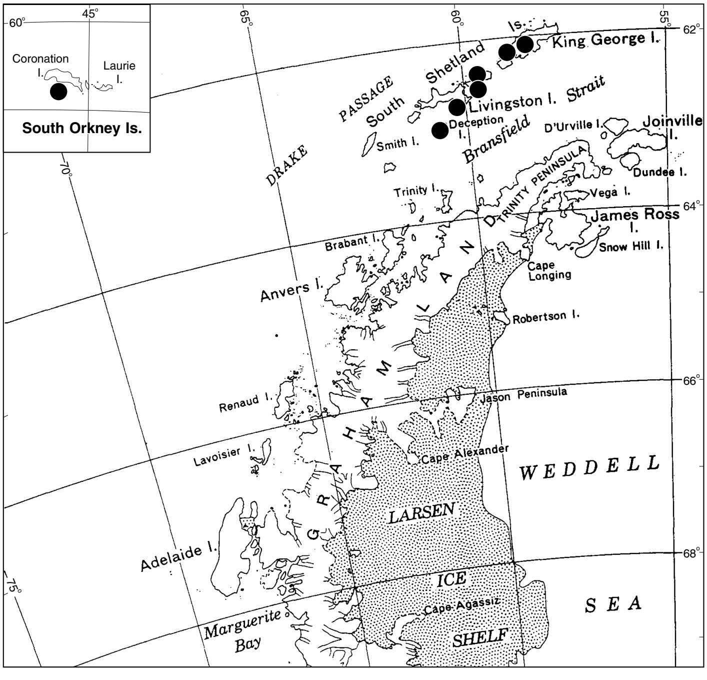

FIGURE 37. Distribution of *Cephaloziella hispidissima* in the Antarctic.

Literature records. — SOUTH ORKNEY ISLANDS: Signy Island (Ochyra & Váňa, 1989*a*: 196). SOUTH SHETLAND ISLANDS: King George Island (Ochyra & Váňa, 1989*a*: 196, 1989*b*: 215; Myrcha *et al*., 1991: 163); Livingston Island (Schuster, 1969*a*: 103; Ochyra & Váňa, 1989*b*: 215; Sancho *et al*., 1999: 321).

2. ***Cephaloziella varians*** (Gottsche) Steph. Fig. 38

Cephaloziella varians (Gottsche) Steph., Wiss. Erg. Schwed. Südpol. Exp. 1901–1903, **4**(1): 4. 1905. – *Jungermannia varians* Gottsche *in* Neumayer, Deutsch. Exp. Int. Polarforsch. **2**: 452. 1890. – *Cephalozia varians* (Gottsche) Steph., Résult. Voy. S.Y. Belgica 1897–1899 Rap. Sci. **6**(5): 5. 1901. – *Lepidoziella varians* (Gottsche) Mahu, Bol. Antárt. Chileno **7**: 3. 1987, *comb. inval.* – Type: Dr Will Nr. 35. Süd-Georgien, Bachgrund oberhalb der Pinguinbay. 26. Januar 1883 [Holotype: "Herbarium Regnum Monacense. Cephaloziella varians (Gottsche) Nº 35 varia. Jungermannia varians G. Original Gottsche Rasen 5. Bachgrund oberhalb der Pinguinbay Süd-Georgien 26/I 83 W. leg. Will" – M!].

Cephaloziella arctica Bryhn & Douin *ex* Müll. Frib., Leberm. Deutschl. **2**: 159, *f. 45*. 1913. – *Cephalozia divaricata* (Sm.) Schiffn. var. *verrucosa* C. E. O. Jensen, Medd. Grønland **15**: 374, *fig*. 1898. – *Cephalozia verrucosa* (C. E. O. Jensen) Bryhn & Kaal. *in* Bryhn, Rep. Sec. Norw. Arct. Exp. Fram 1898–1902, **2**(11): 45. 1906. – *Cephaloziella verrucosa* (C. E. O. Jensen) Bryhn & Kaal. *in* Bryhn, Skr. Vidensk.-Selsk. Christiana Math.-Naturvidensk. Kl. **1908**(5): 4. 1908, *hom. illeg.* [non *C. verrucosa* Steph., Hedwigia **32**: 318. 1892]. – Type: East Greenland, Scoresby Sound, 1892, N. Hartz [Holotype: C (*non* vidi); isotypes: BR-douin!, S!]. First synonymised by Ochyra and Váňa (1989*a*: 196).

Cephaloziella antarctica Douin, Mém. Soc. Bot. France **29**: 78. 1920. – Type: Rég. ant. [Lectotype (***nov.***): "Exemplaire original du Cephaloziella antarctica Douin (ex herb. Stephani) nº 1. Ex herb. Steph. Cephalozia Steph. Jungermannia varians G. Terres antarcticques Canal de la Belgique, sur les rochers isolées au milieu d'un glacier à som – XX^{e} débarq^{t} 267^{b} Exp. ant. belge. 12 fev 98" – BR-douin!; isotypes: BR!, G-steph (*non vidi*)], ***syn. nov.***

Cephaloziella varians (Gottsche) Steph. fo. *minor* Grolle, Br. Antarct. Surv. Bull. **28**: 83. 1972, *nom. nud.* – Original material: South Sandwich Islands, Candlemas Island, western end of eastern lagoon, *Longton 597* – AAS!, KRAM!, ***syn. nov.***

Plants small and delicate, green, yellow-green to brown-green, deep violet to red-brown or black (especially far southern populations), slightly lustrous, in compact patches or intermixed among other bryophytes. *Stems* 2–8(–12) mm long and about 150–350 μm wide, creeping to suberect, simple or sparsely lateral-intrcalary branched, brownish, rather rigid, 70–80 μm in diameter, in transverse section with thin- to strongly thick-walled cortical cells surrounding somewhat smaller medullary cells. *Rhizoids* hyaline, rare or relatively common, at least at the stem base. *Leaves* transversely to subtransversely inserted, mostly distant, rarely approximate, suberect to patent, plane to concave, 0.1–0.25 mm long, mostly about 1.5–2 times as wide as the stem, bilobed to 0.5–0.7 of the length; lobes ovate to ovate-triangular, erect or incurved, acute to rounded, entire-margined, 6–10 cells broad at base, with sharp sinus; leaf cells small, 12–15 × 10–13 μm, thin- or slightly thick-walled; cuticle smooth or slightly verrucose. *Underleaves* present, small and lingulate to lanceolate or bilobed. *Pseudodioecious* or *autoecious*, but mostly sterile (in Antarctica). *Male inflorescence* terminal, becoming intercalary; *male bracts* imbricate, in 4–10 pairs, saccate at base, monandrous. *Female inflorescence* on elongate shoots; female bracts broadly ovate, nearly entire-margined; bracteoles mostly bilobed, smaller than the bracts. *Perianth* obloid to obloid-clavate, in the apical region formed of slightly to moderately thick-walled, rectangular cells, decolorate in apical 1–3 rows, cells in the lower part quadrate to short-rectangular, firm-walled. *Capsule* ovoid-elliptical with straight, valves rounded at apices, with bistratose walls; epidermal cells with nodular thickenings in surface view; inner cell layer with semiannular, narrow bands. *Spores* small, 9–12 μm in diameter, delicately verruculose; elaters free, bispiral, 7–8 μm in diameter; spore/elater width ratio 1.1–1.5 : 1.

Taxonomic and nomenclatural notes. — *Cephaloziella varians* was originally described as *Jungermannia varians* by Gottsche (1890) from material collected by H. Will on South Georgia during the German Polar Year Expedition of 1882–1883. Stephani (1901) reported it for the first time from Antarctica on the basis of a specimen collected by E. Racovitza in the Gerlache Strait during the Belgian Antarctic Expedition of 1897–1899 and, at the same time, he transferred it to *Cephalozia* as *C. varians* (Gottsche) Steph. Later, Stephani (1905) moved this species to *Cephaloziella* and this placement was generally accepted by hepaticologists. Mahu (1987) called this species *Lepidoziella varians* and it is assumed that this is a misprint because he was quoting directly from Broady *et al.* (1987) who reported *Cephaloziella varians* from Mt. Melbourne, Victoria Land. Whatever intention of the author was, this generic name has never been validly published, so the relevant combination *Lepidoziella varians* is also invalid.

The specimens collected by Racovitza in Antarctica were recognised by Douin (1920) as a separate species, *Cephaloziella antarctica*. He provided only the following brief diagnosis in the key to *Cephaloziella* species: "Lobes très larges (10–15 cell.) ayant souvent 1–2 dents basilaires antérieures, séparés par un sinus atteignant la 1/2 env.; feuilles ayant çà et là de grandes dents dorsales; de grands amph.; tiges de 5–10 mm. stériles" and stated that the material came from the Antarctic region. The relevant specimen in the Douin herbarium at BR bears the closer locality data which show that it was collected during the Belgian Antarctic Expedition of 1897–1899. The material agrees well with other Antarctic populations and the type of *C. varians* and therefore these names are here reduced to synonymy, the latter having priority.

Despite the considerable plasticity of the Antarctic plants, no attempts have been made to recognise various phenotypes as separate taxa. Only Grolle (1972*a*) recognised a very minute plant from the South Sandwich Islands as a separate form, fo. *minor*, but he failed to provide its Latin diagnosis, thus invalidly publishing this name. It is here reduced to synonymy with *C. varians* because no discernible differences from other expressions of this species could be found; its diminutive size indicates that it is merely an environmental variant induced by the severe polar conditions.

The taxonomy of the Antarctic populations named as *Cephaloziella varians* was discussed in greater detail by Ochyra and Váňa (1989*a*). These authors concluded

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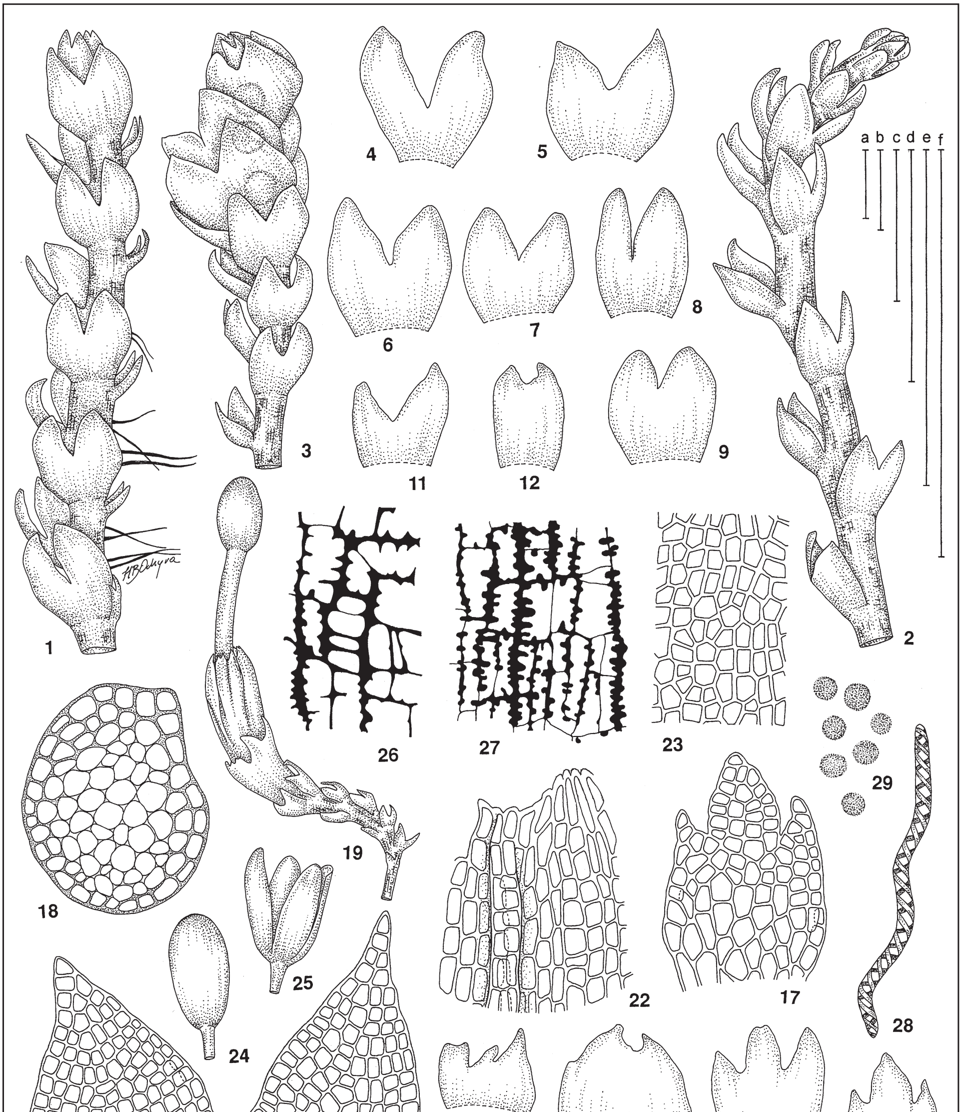
FIGURE 38. *Cephaloziella varians*. **1–3**. Sterile plants. **4–9**. Leaves. **10**. Leaf cells. **11–16**. Underleaves. **17**. Cells of underleaves. **18**. Transverse section of stem. **19**. Perianth-bearing shoot tip. **20**. Antheridium and bracts. **21**. Perianth bract. **22**. Portion of perianth mouth. **23**. Perianth cells in middle part. **24–25**. Sporophytes. **26**. Epidermal cells of capsule wall. **27**. Inner cells of capsule wall. **28**. Elater. **29**. Spores. (1–2, 4–18, 21–23, 26–29 from *Lewis Smith 9118*; 3, 20 from *Convey 226B*; 19, 24–25, from *Lewis Smith 9314*; all in AAS.) Scale bars: a – 0.5 mm (4–7) and 100 µm (15–16); b – 1 mm (1–2) and 0.5 mm (3); c – 1 mm (12–14, 17); d – 100 µm (18–19); e – 1 mm (11); f – 100 µm (8, 10) and 50 µm (20–26); g – 100 µm (9).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that they are inseparable from the Arctic plants known as *C. arctica* and considered both names to be synonymous. In 1967 R. M. Schuster collected an extreme phenotype of *C. arctica* from New Zealand and later described it as subsp. *subantarctica* (Schuster, 1971). It differs from subsp. *arctica* by its very large underleaves (mostly 0.2–0.35 of the leaf size and often bifid), the leaves and female bracts tending to be folded, the abaxial surface of the leaves with occassional faint protrusions and the bases obliquely spreading, and never with the *C. arctica*-type of concave, suberect leaf with incurved lobes. The status of this taxon is in need of a revision as its taxonomic status is still doubtful because of the paucity of the type material (Schuster, 1996*a*).

Schuster and Damsholt (1974) and Schuster (1980*a*) reported *Cephaloziella arctica* from Litchfield Island off the south of Anvers Island, mid-western Antarctic Peninsula, on the basis of fertile plants which, according to these authors, could be considered merely as a geographical race of this species. During the present study, two specimens with gametangia have been detected in the copious material from the South Sandwich Islands and Alexander Island deposited in AAS. In one specimen (*Convey 00226B*) only some young androecia were found, but another specimen (*Lewis Smith 09118*), growing intermixed with *Bryum pseudotriquetrum*, contained many androecia and perianths on long axes. Unfortunately, the lower parts of the stems in this plant are decaying, so the sex condition cannot be stated with certainty. This specimen should be autoecious, but this could not be accurately confirmed.

The problem of the taxonomy of Antarctic and sub-Antarctic populations of "*Cephaloziella exiliflora s. lato*" was simplified by Fulford (1976). This author accepted a very wide concept of *C. exiliflora* and included in this species the Australasian (called *C. exiliflora*), South American (named *C. dusenii* and *C. verrucosa*) as well as Antarctic populations (usually named *C. varians*). Additionally, *C. tristaniana* from Tristan da Cunha and *C. caledonica* from New Caledonia were merged with *C. exiliflora* (the latter concept was presented on the annotating label in FH). This concept is very close to that of Douin (1920) (cf. also Schuster 1996*a*). In contrast to Fulford (1976), Douin (1920) considered *C. exiliflora* as "paroiques, rarement synoiques" or "autoiques", whereas Fulford (1976) referred to dioecious taxa. The problem of the sexuality of the plants is therefore now partially solved, but the other problem of the high plasticity of the plants and their varying ecology remains unresolved.

Thus, the current situation of the complex may be summarized as follows:

1. The Antarctic populations, growing on soil and damp moss-covered rocks, are probably autoecious or pseudodioecious. The plants have mostly reduced, remote leaves, relatively large underleaves, and brownish or greenish colour. Arctic populations of *Cephaloziella varians* are also sometimes reddish or violet, but these colours are seldom found in the Antarctic populations. In our opinion these

plants represent a separate bipolar species for which the oldest available name is *C. varians*, as already suggested by Ochyra and Váňa (1989*a*). It is very common in the Antarctic and very rare elsewhere in more northerly areas (in New Zealand, though, as stated above, the status of the local populations still awaits a taxonomic assessment). Unfortunately, the type of this species is sterile and comprises plants not in optimal phase.

2. The Australasian populations, growing on charred-wood (and also on bark), are also clearly autoecious or pseudodioecious. They differ from the Antarctic populations by having very small, few-celled, often vestigial underleaves, relatively large leaves and mostly red-brown colour. (Typically, they more closely resemble *Allisoniella* than *Cephaloziella*.) Arctic populations of *C. varians* also differ from these plants. In our opinion the Australasian populations represent a separate species, *Cephaloziella exiliflora*, whose type consists of very well-developed fertile plants. Douin (1920; cf. also Schuster, 1996*a*) also placed *C. caledonica* in this taxon, designated as "pl. typica" growing "sur la terre et les places à charbon" and *C. dusenii*, growing "in rupibus" (this statement is considered by Schuster (1963) as incorrect on the basis of the presence of the charcoal on the leaves of the shoots in the type specimen). The isotype of *C. caledonica* (FH) contains pinkish to reddish, autoecious plants, with small leaves and large underleaves which in habit are more similar to *C. varians* than to *C. exiliflora*. Fulford (see above) merged this species with *C. exiliflora*, but we accept this concept with some hesitation.

3. The southern South American populations called *Cephaloziella dusenii* pose another problem. Schuster (1971) discussed this species in detail, concluding that it is dioecious and belongs within *C. divaricata* (=*C. byssacea* according to his approach). He considered this species to be close to *C. exiliflora*, both morphologically and ecologically, and it was probably only on the basis of the different sexuality that he did not synonymise *C. dusenii* with *C. exiliflora* as previously done by Douin (1920) and Fulford (1976). Engel (1978) emphasised that Schuster probably did not see the lectotype of *C. dusenii* (difference in the date). He (Engel, 1978) described the plants of *C. dusenii* from the Brunswick Peninsula and accepted that this species **may** "represent the common and protean circumsubantarctic *C. exiliflora* (Tayl.) Douin – cf. Schuster 1969", but he mentioned the comments on the sexuality of the plants (Schuster, 1971). Engel (1978) also considered *C. verrucosa* Steph. as a separate species differing in the shape of the apical lobe cells and monoecious (autoecious) inflorescence. When discussing this concept in connection with the treatment of *C. exiliflora*, Schuster (1996*a*) gave no additional information on *C. dusenii*. However, he wrote that *C. verrucosa* "surely is not identical with *C. exiliflora*".

The South American populations, at least according to the material examined, are typically much more similar to the Antarctic populations. They have mostly small leaves, relatively large underleaves and are not reddish. Sometimes it is very difficult to separate them from the Antarctic populations on the basis of the morphological characteristics. The sexuality of these plants remains an unresolved problem as there is still no accurate information. Moreover, the treatment of *Cephaloziella* in South America by Fulford (1976) needs careful revision, similar to that made by Schuster (1996*a*) for New Zealand.

At present we treat the Antarctic populations as *Cephaloziella varians*, as already suggested by Ochyra and Váňa (1989*a*). Following the concept of Schuster (1996*a*) *C. exiliflora* is probably a separate species occurring only in the Australasian region. The identity of South American populations called *C. dusenii* and *C. verrucosa* (and probably bearing other synonymous names) still needs careful investigation. If the conspecificity of the South American and Antarctic populations could be confirmed, it would not affect the nomenclature since *C. varians* is the oldest available name in this complex in this region, and it would result only in extension of its geographical range to mainland South America.

Differentiation. — *Cephaloziella varians* is exceptionally variable in colour, morphology and ecology, but several uniform phenotypic characters enable its identity. It is easily distinguished from *C. hispidissima*, the only other species of the genus in this region, by its entirely smooth stems and leaves.

Reproduction in Antarctica. — Populations are almost entirely sterile, but fertile plants have been found very occasionally. Sporophytes have been noted regularly in certain populations in the Marguerite Bay area since 1995. This may be a response to changing climate conditions.

Habitat. — The species occurs predominantly in moist to relatively wet habitats, commonly as a component of communities dominated by turf- and carpet-forming mosses such as *Brachythecium austrosalebrosum*, *Chorisodontium aciphyllum*, *Polytrichastrum alpinum*, *Polytrichum strictum*, *Sanionia georgico-uncinata*, *Warnstorfia laculosa* and *W. sarmentosa*. Its filamentous, thread-like shoots are nearly always present among shoots of mosses, but occasionally larger patches, up to several square metres, grow over the surface of moss where it has become moribund. The species is common on well drained or permanently moist to wet habitats on level or gently sloping ground, on stabilized scree, in wet depressions, along rills, melt water channels and seepage areas, less frequently on soil-covered rock ledges, in rock crevices and fissures, on wet or moist soil among boulders on raised beaches, and sometimes over or between rocks in rather drier sites. It is a constant associate in *Chorisodontium aciphyllum-Polytrichum strictum* turf banks and commonly occurs with *Barbilophozia hatcheri* and *Lophozia excisa*.

World range. — A bipolar species, probably pan-Holarctic in the Northern Hemisphere (Fig. 39). It probably has a continuous arctic distribution, extending in North America to Lake Superior (Schuster, 1980*a*), occurring throughout Iceland, much of Fennoscandia (Söderström, 1995) and Arctic Russia (Schljakov, 1979), recurring in continental Europe to the Pyrenees, Alps and Carpathians, but the Asian distribution poorly known. In the Southern Hemisphere it is common throughout the Antarctic and on South Georgia (from where it was originally described; Gottsche, 1890), Heard Island (Bergstrom & Selkirk, 1997), and also once reported from South Island, New Zealand, but the status of these plants still needs taxonomic evaluation from more copious collections (Schuster, 1996*a*).

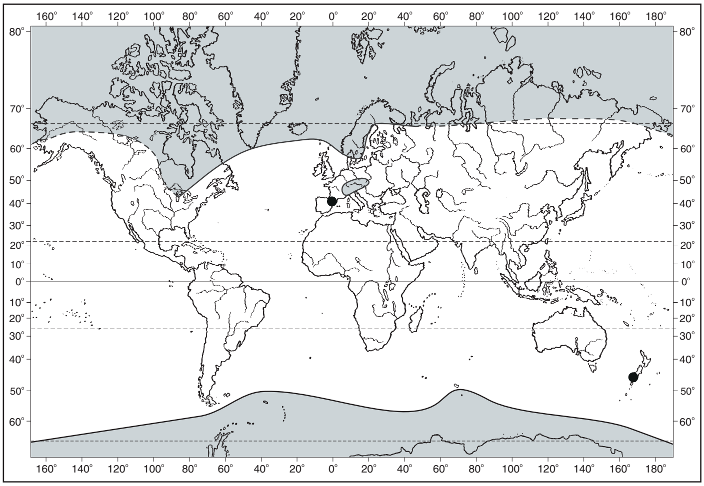


FIGURE 39. Global distribution of *Cephaloziella varians*.

Distribution in Antarctica. — *Cephaloziella varians* is the commonest, most widespread and the most abundant species of liverwort in Antarctica. It is the only liverwort known to occur in the Continental Antarctic where it is widely distributed but scattered in Victoria Land (to Cape Geology, Botany Bay, lat. 77^{o}S), as well as at coastal sites in Wilkes and Princess Elizabeth Lands (Fig. 40). In addition, it is widespread throughout the maritime Antarctic from Bouvetøya and the South Sandwich Islands to lat. 71^{o}50'S on Alexander Island (Fig. 41). Altitudinal range is from sea level to 500 m.

Specimens examined. — BOUVETØYA. Nunatak ridge east of Rustadkollen, *ca* 290 m, *Engelskjøn 200* (BG) and 295 m, *Engelskjøn 200* (BG); Rustadkollen, south-west side at summit, *Engelskjøn 36* (AAS); Moseryggen, 260–287 m, *Engelskjøn 405* (BG).

SOUTH SANDWICH ISLANDS. **LESKOV ISLAND**. Summit ridge, *ca* 100 m, *Convey 245G* (AAS, KRAM) and *ca* 200 m, *Longton 505 & 515A* (AAS, KRAM); east side of the summit ridge, *Convey 249F & 250B* (AAS, KRAM); north slope, *ca* 35 m, *Holdgate 837A* (AAS, KRAM). **VISOKOI ISLAND**. Finger Point, *ca* 35 m, *Longton 763* (AAS, KRAM). **CANDLEMAS ISLAND**. North-west slope of Lucifer Hill, *Convey 226B* (AAS, KRAM); Lucifer Hill, east rim of the south-west crater, *Convey 107F* (AAS, KRAM); Lucifer Hill, north-west ridge, *Convey 230F & 240B* (AAS, KRAM); Lucifer Hill, south edge of shallow gully above Clinker Gulch, *Convey 125D, 126D, 127D, 130C, 151E & 154C* (AAS, KRAM); Clinker Gulch, *Convey 156F, 165A, 181A, 182A, 237B & 238A* (AAS, KRAM); west end of Breakbones Plateau, *Convey 205A, 208B & 210* (AAS, KRAM); Lucifer Hill, north-west ridge active fissure, *Convey 223D, 225C & 226C* (AAS, KRAM); Lucifer Hill, summit of west supporting ridge of gully above Clinker Gulch, *Convey 234C* (AAS, KRAM); west end of eastern lagoon, *ca* 35 m, *Longton 597* (AAS, KRAM); north of eastern lagoon, *ca* 50 m, *Longton 787* (AAS, KRAM); between lagoons and most southerly exposed lava ridge, 65–100 m, *Longton 569* (AAS, KRAM); west shore, south of lagoons, *ca* 35 m, *Longton 586* (AAS, KRAM); north of western lagoon, 50 m, *Longton 693B* (AAS, KRAM). **Montagu Island**. Allen Point, *ca* 50 m, *Convey 100E* (AAS, KRAM). **Bellingshausen Island**. Crater rim west of access point, *ca* 170 m, *Convey 30B & 46H* (AAS, KRAM); south coast, at nearly dead fumaroles, *Convey 75A & 76B* (AAS, KRAM); south slope of main cone, *ca* 25 m, *Holdgate 811B & 839B* (AAS, KRAM), *ca* 100 m, *Holdgate 416A* (AAS, KRAM) and *ca* 135 m, *Holdgate 425B* (AAS, KRAM).

SOUTH ORKNEY ISLANDS. **Monroe Island**. South-west part, *ca* 35 m, *McManmon 68B* (AAS, KRAM). **Coronation Island**. Meier Point, 10 m, *Lewis Smith 8027* (AAS) and 15–35 m, *Lewis Smith 587* (AAS, KRAM); Mansfield Point, *ca* 15 m, *Lewis Smith 298A* (AAS, KRAM) and 10–20 m, *McManmon 15* (AAS); Cape Vik, 100 m, *Lewis Smith 564 & 573F* (AAS, KRAM); Cape Hansen, 20–200 m, *Lewis Smith 3242* (AAS); Shingle Cove, 1.5–2 m, *Lewis Smith 8234* (AAS) and *ca* 65 m, *Lewis Smith 127* (AAS); Sunshine Glacier, 175 m, *Webb 155* (AAS); Olivine Point, *ca* 35 m, *Lewis Smith 133A & 134C* (AAS, KRAM); Saunders Point, *ca* 15 m, *Lewis Smith 25C* (AAS) and *ca* 35 m, *Lewis Smith 18AB* (AAS, KRAM); opposite Saunders Point, 8 m, *Lewis Smith 31A* (AAS, KRAM). **Lynch Island**. North facing bank, *ca* 13 m, *Lindsay 942D & 971* (AAS); without specific locality, 3–35 m, *Lewis Smith 512, 529B & 532B* (AAS, KRAM). **Coffer Island**. West facing rock, 13–15 m, *Cameron & Kennett 9C* (AAS). **Matthews Island**. Promontory north of Coffer Island, *ca* 35 m, *Lewis Smith 191A* (AAS, KRAM). **Powell Island**. Promontory on the west side of Falkland Harbour, *ca* 35 m, *Lewis Smith 278 & 279B* (AAS, KRAM); promontory on south-east coast, *ca* 135 m, *Lewis Smith 205C & 206B* (AAS, KRAM); promontory on east side of Falkland Harbour, *Lewis Smith 54B* (AAS); south-east coast, *ca* 135 m, *Lewis Smith 206B* (AAS). **Christoffersen Island**. Falkland Harbour, 60 m, *Richard 203 & 221B* (AAS, KRAM); southern end, 50 m, *Richard 188B, 190A & 242B* (AAS, KRAM). **Laurie Island**. Cape Geddes *ca* 335 m, *McManmon 204* (AAS); Cape Dundas, *ca* 65 m, *McManmon 184* (AAS); Martin Point, 27 Dec 1952, *Kühnemann s.n.* (BA) and Dec 1962, *Bellisio s.n.* (BA); Cabo Moneta, 200 m, Dec 1962, *Bellisio s.n.* (BA); Punta Diebel, Dec 1962, *Bellisio s.n.* (BA). **Signy Island**. Porteous Point, 50 m, *Lewis Smith 8676B* (AAS); ridge north-east of Thulla Point, 30 m, *Lewis Smith 405* (AAS, KRAM) and 50 m, *Lewis Smith 500B* (AAS, KRAM); south-east of Foca Cove, *Lewis Smith 1850* (AAS, KRAM); Foca Cove, *Lewis Smith 1792* (AAS, KRAM) and 30 m, *Lewis Smith 10913* (AAS, KRAM); Foca Point, 50 m, *Lewis Smith 502C* (AAS); above Spindrift Rocks, 50 m, *Holdgate 760 & 762B* (AAS); between Spindrift Rocks and North Point, *Holdgate 85* (AAS); North Point, *ca* 65 m, *Holdgate 18* (AAS, KRAM); south-east of North Point, *ca* 65 m, *Lewis Smith 685* (AAS, KRAM); west of Mirounga Cove, 10 m, *Lewis Smith 385A* (AAS, KRAM); Mirounga Flats, 10 m, *Lewis Smith 385B* (AAS); Heywood Lake, 8 m, *Lewis Smith 7120* (AAS); Knob Lake, 15 m, *Lewis Smith 5219* (AAS, KRAM); Marble Knolls, near Pumphouse Lake, 10 m, *Lewis Smith 10797B* (AAS, KRAM) *& 5217 & 5220* (AAS, KRAM); Changing Lake,

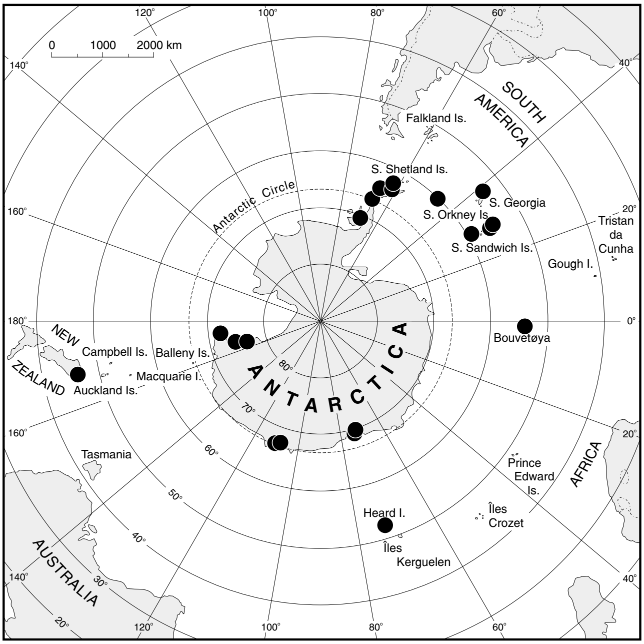


FIGURE 40. Distribution of *Cephaloziella varians* in the Southern Hemisphere.

40 m, *Lewis Smith 10795* (AAS, KRAM); Moss Lake, 50 m, *Lewis Smith 10759* (AAS, KRAM); Limestone Valley, 15 m, *Lewis Smith 5216* (AAS, KRAM); Berntsen Point, *ca* 15 m, *Holdgate 730* (AAS, KRAM) and 50 m, *Taylor 347* (AAS); Factory Cove, south of the base, 100 m, *Lewis Smith 470A* (AAS, KRAM); Factory Cove, slope behind the base, 8 m, *Holdgate 25* (AAS) and 10 m, *Lewis Smith 370A* (AAS, KRAM), *ca* 15 m, *Longton 845* (AAS), *ca* 35 m, *Lewis Smith 622B* (AAS, KRAM) and *Holdgate 50* (AAS, KRAM), 50 m, *Lewis Smith 306* (AAS, KRAM) and 75 m, *Lewis Smith 5198A & 5214B* (AAS) *& 5201A* (AAS, KRAM); Factory Cove, north face of bluffs, *ca* 15 m, *Holdgate 134* (AAS); overlooking Factory Cove, *Taylor 406* (AAS, KRAM); cliffs above Paal Harbour and Rusty Bluff, 80 m, *Lewis Smith 5193A, 5195 & 5197* (AAS, KRAM); Factory Bluffs, 110 m, *Lewis Smith 10891C* (AAS); hill between Factory Cove and Paal Harbour, *ca* 100 m, *Holdgate 36* (AAS, KRAM); Observation Bluff, 10 m, *Holdgate 68* (AAS, KRAM) and 15 m, *Holdgate 75B* (AAS); Polynesia Point, 25 m, *Holdgate 71 & 72B* (AAS) and 20–30 m, *Holdgate 667* (AAS); above Paal Harbour, *ca* 15 m, *Holdgate 757B* (AAS, KRAM), *ca* 35 m, *Holdgate 751CC* (AAS, KRAM), 70 m, *Lewis Smith 10862 & 10863* (AAS, KRAM), *ca* 80 m, *Lewis Smith 683B* (AAS, KRAM) *& 5195, 5196B & 5197* (AAS), *ca* 85 m, *Lewis Smith 682B* (AAS, KRAM) and without elevation, *Lewis Smith 1449* (AAS, KRAM); east side of Rusty Bluff above Paal Harbour, 50 m, *Lewis Smith 8221* (AAS, KRAM), 75 m, *Lewis Smith 10862* (AAS, KRAM), 80 m, *Lewis Smith 5193A* (AAS) and 100 m, *Lewis Smith 351A* (AAS, KRAM) *& 352B* (AAS, KRAM); west of Rusty Bluff, *Lewis Smith 1853* (AAS, KRAM); Moraine Valley, *ca* 35 m, *Lewis Smith 696* (AAS, KRAM); upper Moraine Valley, 60 m, *Lewis Smith 5222* (AAS, KRAM) and 75 m, *Lewis Smith 10852* (AAS, KRAM); between Lenton and Rethval Points, *ca* 15 m, *Holdgate 102* (AAS); knoll inland from Re-

thval Point, 50 m, *Holdgate 105C* (AAS); Hillier Moss, *Lewis Smith 1851* (AAS, KRAM); Gourlay Peninsula, *ca* 35 m, *Lewis Smith 358A* (AAS, KRAM); between Gourlay Peninsula and Lenton Point, *ca* 35 m, *Lewis Smith 476B* (AAS, KRAM); Lenton Point, *ca* 13 m, *Holdgate 686* (AAS) and *ca* 35 m, *Holdgate 711B* (AAS); Lenton Point, *ca* 13 m, *Holdgate 686* (AAS) and *ca* 35 m, *Holdgate 711B* (AAS); Western Oliphant Islands, 30 m, *Lewis Smith 5221* (AAS, KRAM). **Moe Island**. Without closer locality data, 200 m, *Lewis Smith 5243B* (AAS, KRAM) and 5–200 m, *Lewis Smith 5263* (AAS, KRAM).

SOUTH SHETLAND ISLANDS. **Elephant Island**. 2 km south-west of Endurance Glacier, 167 m, *Allison 22F* (AAS); 0.5 km south-west of Endurance Glacier, 183 m, *Allison 152B & 179B* (AAS) and 305 m, *Allison 241F* (AAS); Stinker Point, 61 m, *Allison 77B* (AAS) and 122 m, *Allison 91B* (AAS); 3 km south-west of Walker Point, *Allison 184B* (AAS). **O'Brien Island**. Near north-east coast, 150–180 m, *Baylis 49* (AAS). **King George Island**. ***Bransfield Strait***. Red Hill, 100 m, *Ochyra 1085/80* (KRAM, PRC); Blue Dyke, 120 m, *Ochyra 1155A/80* (KRAM, PRC); Bastion, 240 m, *Ochyra 991/80* (KRAM, PRC); Uchatka Point, 20 m, *Ochyra 1054/80* (KRAM, PRC). ***Admiralty Bay***: Demay Point, 50 m, *Ochyra 1335/80* (KRAM, PRC); Creeping Slopes, 60 m, *Ochyra 1248/80* (KRAM, PRC) and 120 m, *Ochyra 1277/80* (KRAM, PRC); Agat Point, 15 m, *Ochyra 372/80* (KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 99]; Siodło Hill, 85 m, *Ochyra 776/80* (KRAM, PRC) and 130 m, *Ochyra 773/80* (KRAM, PRC); Sphinx Hill, 95 m, *Ochyra 224/80* (KRAM, PRC), 115 m, *Ochyra 190/80* (KRAM, PRC) and 120 m, *Ochyra 212/80* (KRAM, PRC); Czajkowski Needle, 260 m, *Ochyra 664/80* (KRAM, PRC); Rescurs Hills, 25 m, *Ochyra 4966/79* (KRAM, PRC), 45 m, *Ochyra 1482/80* (KRAM, PRC) and 60 m, *Ochyra 4888/79* (AAS, KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 148]; Ornithologist's Creek, 15 m, *Ochyra 709/80* (KRAM, PRC) and 170 m, *Ochyra 4968/79* (AAS, KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 200]; Jasnorzewski Gardens, 4 m, *Ochyra 1486/80* (AAS, KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 74] *& 1490/80* (KRAM, PRC); Hala, 20 m, *Ochyra 5199/79* (KRAM, PRC); Ambona, 80 m, *Ochyra 1606/80 & 1637/80* (KRAM, PRC); Ubocz, 95 m, *Ochyra 4962/79* (KRAM, PRC), 115 m, *Ochyra 2377/80* (KRAM, PRC) and 125 m, *Ochyra 2373/80* (KRAM, PRC); Penguin Ridge, 52 m, *Ochyra 1409/80* (AAS, KRAM, PRC) [*Bryophyta Selecta Exsiccata* No. 100]; Jersak Hills, 100 m, *Ochyra 5071/79* (KRAM, PRC) and 180 m, *Ochyra 5141/79* (KRAM, PRC); Jardine Peak, 275 m, *Ochyra 5156/79* (KRAM, PRC) *& 5158* (AAS, KRAM, PRC) [*Bryophyta Selecta Exsiccata* No. 753]; unnamed hills on Wróbel Glacier, 130 m, *Ochyra 647/80* (KRAM, PRC); Italia Valley, 100 m, *Ochyra 95/80* (KRAM, PRC); Klekowski Crag, 220 m, *Ochyra 2311/80* (KRAM, PRC); Komandor Peak, 230 m, *Ochyra 1930/80 & 1951/80* (KRAM, PRC) and 250 m, *Ochyra 1942/80* (KRAM, PRC); Round Hill, 50 m, *Ochyra 538/80 & 543/80* (KRAM, PRC); Keller Peninsula, near the British base, *ca* 12 m, *Lewis Smith 713* (AAS, KRAM); Moraine Point, 3 m, *Ochyra 490/80* (KRAM, PRC); Smok Hill, 25 m, *Ochyra 2055A/80* (KRAM, PRC); Mount Wawel, 40 m, *Ochyra 2166/80* (KRAM, PRC); Point Hennequin, 10 m, *Ochyra 2243/80* (KRAM, PRC); Basalt Point, 15 m, *Ochyra 2232/80* (KRAM, PRC); Bell Zygmunt, 300 m, *Ochyra 2685/80* (KRAM, PRC); Vauréal Peak, 35 m, *Ochyra 5250/79* (KRAM, PRC). ***Barton Peninsula***: Without specific locality, *Jabłoński 206* (KRAM); south beacg, 3 m, *Lindsay 716* (AAS). ***Fildes Peninsula***: Ardley Island, 10 m, *Ochyra 2484/80* (KRAM, PRC) and 30 m, *Ochyra 24470* (KRAM, PRC), *Kühnemann 35* (AAS, KRAM) and *Komárková 280 & 563*

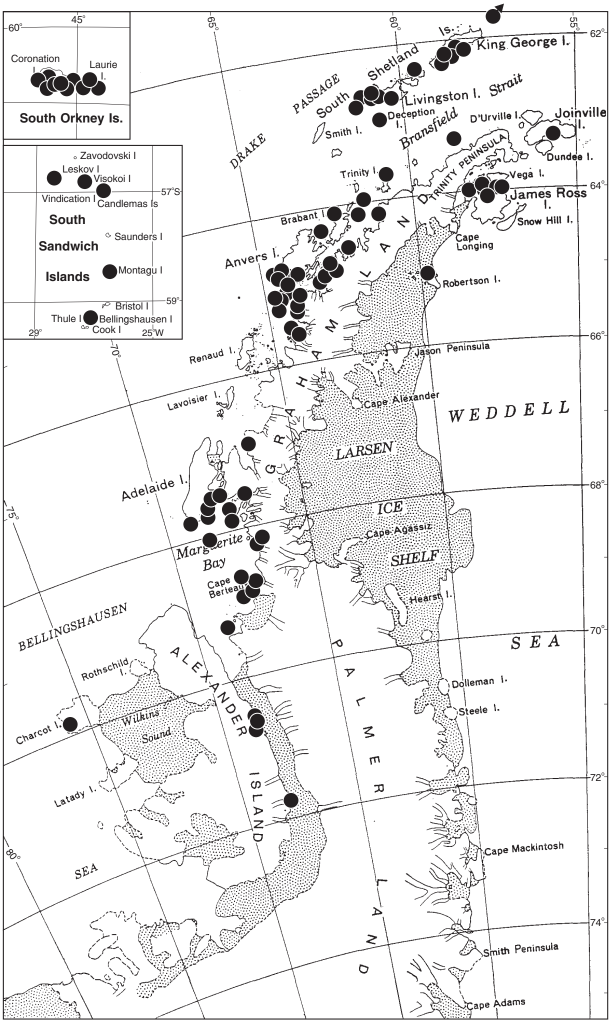


FIGURE 41. Distribution of *Cephaloziella varians* in the maritime Antarctic. The localities on Elephant and O'Brien Islands are indicated by an arrow.

(KRAM); Bukhta Kamenistaya, *Nikolaev 35* (LE, PRC). **Nelson Island**. Harmony Cove, 25 m, *Lindsay 683* (AAS); without specific locality, *Komárková 1067* (KRAM). **Robert Island**. Coppermine Cove, 8–35 m, *Lewis Smith 929* (AAS, KRAM). **Livingston Island**. ***Byers Peninsula***: Clark Nunatak, 180 m, *Lindsay 215* (AAS) *& 224BB* (AAS, KRAM); Ocoa Point, 20–75 m, *Richard 44A* (AAS, KRAM); opposite Astor Island, *Lindsay 345* (AAS); South Beaches, Vietor Rock, *Lindsay 462* (AAS); between Chester Cone and Sealers Hill, *Lewis Smith 3824 & 3825* (AAS, KRAM); extreme end of South Beaches, 17 m, *Lindsay 445B* (AAS). ***Hurd Peninsula***: South Bay, near Spanish Base Juan Carlos I, 5 m, *Schulz 175* (Hb. Schulz, KRAM). **Snow Island**. President Head, 5–10 m, *Richard 11B* (AAS, KRAM). **Deception Island**. South-westn of Ronald Hill, *ca* 12 m, *Lewis Smith 84* (AAS, KRAM); north-east of the British base, *ca* 15 m, *Lewis Smith 739* (AAS, KRAM);

Whalers Bay, 8 m, *Lewis Smith 3633* (AAS, KRAM) and *ca* 15 m, *Longton 887* (AAS); Fumarole Bay, 8–30 m, *Lewis Smith 3633* (AAS); Crater Lake, 15 m, *Lewis Smith 5646D, 5647D, 5648C, 5650C & 5660G* (AAS); Stonethrow Ridge, 45–230 m, *Lewis Smith 5809G* (AAS); Vapour Col, 100 m, *Lewis Smith 5619B* (AAS) and *Mason 22B* (AAS, KRAM); Kendall Terrace, *Lewis Smith 5742E* (AAS); small lake to north-east of Mt. Kirkwood, 200 m, *Lewis Smith 5723C* (AAS); summit of peak 2.2 km west-north-west of Mt. Kirkwood, 350 m, *Mason 123B* (AAS, KRAM).

WEST ANTARCTIC PENINSULA. **Trinity Peninsula**. Joinville Island, Mt. Alexander, 15–50 m, *Lewis Smith 3703* (AAS) and 60 m, *Lewis Smith 3672B* (AAS, KRAM); Astrolabe Island, *Lewis Smith 6976B* (AAS) and 50–70 m, *Lewis Smith 4098* (AAS). **Davis Coast**. Trinity Island, 200 m, *Willey & G. Smith s.n. (Lewis Smith 700D)* (AAS, KRAM). **Danco Coast**. Centre Rocks, 7 Feb 1952, *Hässel de Menendez s.n.* (BA); Cuverville Island, 10–50 m, *Lewis Smith 4211* (AAS); Cierva Point, *Komárková 615* (KRAM); Coughtrey Peninsula, Almirante Brown Station, 17 Dec 1954, *Kühnemann s.n.* (BA); Stony Point, 21 Feb 1952, *Popovici s.n.* (BA); Lemaire Channel, *Racovitza 267B* (BR – type of *Cephaloziella antarctica*). ***Palmer Archipelago***: Christiania Islands, Intercurrence Island, *ca* 7 m, *Brown 1E* (AAS). ***Melchior Archipelago***: Omega Island, Canal Murature, 20–25 m, *Frolick 4* (AAS, KRAM); ***Brabant Island***: Metchikoff Point, 100 m, *Hankinson 31B* (AAS); without closer locality data, *Hankinson 201F* (AAS); Two Hummock Island, *Lewis Smith 704F* (AAS). ***Anvers Island***: Norsel Point, *Komárková 1067* (KRAM); Palmer Station, 10–15 m, *Lewis Smith 748* (AAS, KRAM); Litchfield Island, *Komárková 72, 84, 497, 504, 505, 1103 & 1106* (KRAM), *ca* 7 m, *Corner 375C* (AAS), *ca* 15 m, *Corner 391* (AAS, KRAM) and *ca* 25 m, *Corner 368* (AAS); largest of Joubin Islands, 20–50 m, *Lewis Smith 1989* (AAS); Hermit Island, 15–25 m, *Lewis Smith 888 & 891C* (AAS, KRAM); Shortcut Island, *Komárková 58B & 1056* (KRAM); Dream, Island, *Komárková 667, 982, 992 & 1001* (KRAM); Laggard Island, *ca* 15 m, *Longton 1297* (AAS, KRAM); Cormorant Island, 21 m, *Scott 21* (AAS). **Graham Coast**. Rasmussen Island, *Lewis Smith 1927* (AAS, KRAM); Cape Tuxen, 15 m, *Fowbert 31* (AAS, KRAM), *ca* 65 m, *Corner 850C* (AAS, KRAM), 30–300 m, *Lewis Smith 4915* (AAS, KRAM) and *ca* 335 m, *Corner 684B* (AAS, KRAM). ***Petermann Island***: North end, 20 m, *Corner 790C* (AAS) and *ca* 35 m, *Corner 794* (AAS). ***Argentine Islands***: Galindez Island, Stella Creek, 10 m, *Corner 443* (AAS, KRAM), *ca* 15 m, *Corner 489* (AAS) and *ca* 25 m, *Corner 418 & 441B* (AAS, KRAM); Winter Island, *ca* 3 m, *Taylor 125* (AAS); Uruguay Island, *ca* 20 m, *Corner 739A* (AAS, KRAM) and *ca* 25 m, *Corner 439A* (AAS, KRAM); largest island between Irizar and Uruguay Islands, 10 m, *Corner 698A* (AAS, KRAM); Skua Island, Skua Creek, *ca* 6 m, *Corner 778C* (AAS) and *ca* 8 m, *Corner 456A & 459* (AAS); Corner Islands, *ca* 13 m, *Corner 581* (AAS, KRAM) and *ca* 16 m, *Corner 780* (AAS). ***Roca Islands***: Largest island of the group, *Lewis Smith 2478* (AAS); small island near the middle of the group, 40 m, *Lewis Smith 2018* (AAS, KRAM). ***Grandidier Channel***: Sommerville Island, *Taylor 114B* (AAS); Lahille Island, 2–5 m, *Lewis Smith 4330 & 4350* (AAS, KRAM); largest island off Takaki Point, 10–35 m, *Lewis Smith 4350* (AAS); Takaki Point, 5–20 m, *Lewis Smith 4392* (AAS, KRAM). **Loubet Coast**. Orford Cliff, *Lewis Smith 5271B* (AAS); Blaiklock Island, 5 m, *Brown 13B* (AAS) and 8–10 m, *Lewis Smith 850* (AAS, KRAM); Piñero Island, 10–25 m, *Lewis Smith 4833* (AAS); Dismal Island, 5–25 m, *Lewis Smith 3474 & 3531* (AAS). ***Léonie Islands***: Lagoon Island, 5 m, *Lewis Smith 9151B* (AAS), 10 m, *Lewis Smith 3596C* (AAS), 20–25 m, *Lewis Smith 9184* (AAS) and 20–35 m, *Lewis Smith 9177* (AAS); Anchorage Island, 25–35 m, *Lewis Smith 9206* (AAS); north side of Léonie Island, 20 m, *Lewis Smith 8998B* (AAS, KRAM), 25 m, *Lewis Smith 9118* (AAS, KRAM) and 30 m, *Lewis Smith 8927E & 8960* (AAS). **FALLIÈRES COAST**. Adelaide Island, near the Rothera Station, 10 m, *Lewis Smith 771* (AAS, KRAM); same locality, Rothera Point, 5 m, *Lewis Smith 8920* (AAS) and 7 m, *Fenton 39B* (AAS, KRAM), 17 m, *Fenton 30B* (AAS, KRAM), 20–30 m, *Lewis Smith 1875B* (AAS, KRAM) and 25 m, *Fenton 50C* (AAS, KRAM); Pourquoi-Pas Island, Dalgleish Bay, 5–20 m, *Lewis Smith 4775* (AAS, KRAM); Avian Island, *ca* 15 m, *Longton 938B* (AAS) and *Lewis Smith 103* (AAS, KRAM); Jenny Island, *Killingbeck 111BB, 228B & 229BB* (AAS, KRAM) and 15–50 m, *Lewis Smith 4709B & 4720* (AAS, KRAM); Laubeuf Fjord on east side of Jenny Island, *ca* 22 m, *Taylor 428* (AAS) and *ca* 26 m, *Tylor 442C* (AAS); Lagotellerie Island, *ca* 50 m, *Lewis Smith 1772 & 4844B* (AAS, KRAM); island in north-west of Faure Islands, 5–10 m, *Lewis Smith 3512* (AAS, KRAM); north-east side of Neny Island, 8–35 m, *Lewis Smith 794* (AAS, KRAM) and 50 m, *Lewis Smith 795* (AAS, KRAM); Roman Four Promontory, 10–30 m, *Lewis Smith 4567B & 4568* (AAS); largest of the Refuge Islands, 10–25 m, *Lewis Smith 4520* (AAS); Flyspot Rocks, *Poncet 2B* (AAS); Alamode Island, *Poncet 3H* (AAS); Terra Firma Islands, *ca* 10 m, *BAS Misc. 216* (AAS, KRAM); Mushroom Island, *Poncet 1DD* (AAS, KRAM); Mica Islands, *Wynn-Williams 144C* (AAS). **GEORGE VI SOUND**. ***Alexander Island***: Ablation Point, *Heywood & Light 83 & 87* (AAS, KRAM); Ablation Valley, west shore of Ablation Lake, 2–3 m, *Lewis Smith 9224C, 9249, 9251D, 9252B, 9253B, 9264, 9266C, 9267B, 9270D, 9271C, 9272C, 9275D & 9277C* (AAS, KRAM); same locality, south-west side of Ablation Lake, *Lewis Smith 8842D, 9313C & 9314* (AAS, KRAM); same locality, near red rock, *Lewis Smith 8842D* (AAS); Moutonée Valley, *Heywood & Light 76* (AAS, KRAM); Mars Glacier, Natal Ridge, *Lewis Smith 8851D* (AAS). ***Charcot Island***: Marion Nunataks, 85 m, *Lewis Smith 10496A, 10507A & 10529A* (AAS, KRAM).

EAST ANTARCTIC PENINSULA. **TRINITY PENINSULA**. ***James Ross Island***: Lachmann Crags, 5–35 m, *Lewis Smith 7327A & 7333D* (AAS) and 35 m, *Lewis Smith 7381D & 7385A* (AAS, KRAM); Andreassen Point, 10 m, *Lewis Smith 7611A* (AAS, KRAM); south side of St. Martha Cove, 150 m, *Lewis Smith 7512* (AAS, KRAM); lower valley to north of St. Martha Cove, 50 m, *Lewis Smith 7512* (AAS); Dreadnought Point, 10 m, *Lewis Smith 7501* (AAS, KRAM); Blancmange Hill, 12–15 m, *Lewis Smith 7679A* (AAS, KRAM); Fortress Hill, 150 m, *Lewis Smith 7775A* (AAS); Terrapin Hill, 200 m, *Lewis Smith 7735A* (AAS); Holluschickie Bay, Kotick Point, 100 m, *Lewis Smith 5472D* (AAS). ***Vega Island***: north end of False Island Point, 25–30 m, *Lewis Smith 7828A* (AAS, KRAM). **NORDENSKJÖLD COAST**. Oceana Nunatak, 100 m, *Lewis Smith 6430C* (AAS).

EAST ANTARCTICA. PRINCESS ELIZABETH LAND. **INGRID CHRISTENSEN COAST**. ***Larsemann Hills***: Bermesat, *Seppelt 8014* (ADT); 1 km west of Law Base, *Seppelt 20030* (ADT); Progress Ridge, above Progress Lake, *Pidgeon LH 78–3* (ADT); Stornes Peninsula, *Pidgeon LH 31–3* (ADT); north-east end of the Stornes Peninsula, *Pidgeon LH 45–3* (ADT). ***Bolingen Islands***: north side of centre of Vogöy Island, *Pidgeon VI 5–9* (ADT). WILKES LAND. **BUDD COAST**. ***Windmill Island***: Clark Peninsula, 15 m, *Seppelt 13653* (ADT) and 20 m, *Seppelt 13535* (ADT); same locality, Løken Moraine east of Wilkes Station, 140 m, *Seppelt 13741* (ADT); same locality, north-east of Whitney Point, 25 m, *Lewis Smith 6201B & 6202* (AAS); same locality, hill to east of Wilkes Station, *Lewis Smith 6210*

(AAS); same locality, north-east of Stevenson Cove, 25 m, *Lewis Smith 6226B* (AAS); Mitchell Peninsula, *Seppelt 13280, 13383 & 13386* (ADT); Mitchell Peninsula, Løken Moraine, 20 Dec 1982, *Seppelt s.n.* (ADT); north-west end of Robinson Ridge, *Seppelt 19817* (ADT); Bailey Peninsula, *Seppelt 16135* (ADT) and 35 m, *Seppelt 13226* (ADT); same locality, Haupt Nunataks, 104 m, *Seppelt 13919* (ADT); same locality, O'Brien Bay, *Lewis Smith 6165* (AAS); same locality, SSSI area, *ca* 30 m, *Lewis Smith 6247* (AAS). SOUTHERN VICTORIA LAND. ***Granite Harbour***: Botany Bay, upper beach terrace, *Seppelt 19223* (ADT) and 25 m, *Seppelt 17783* (ADT); Edmondson Point North, 10 m, *Lewis Smith 9612* (AAS); same locality, south of Phormidium Lake, *Lewis Smith 9625* (AAS); same locality, middle terrace of North Valley, *Lewis Smith 9638B* (AAS); same locality, North Valley, 2 m, *Lewis Smith 9647* (AAS) and 75 m, *Lewis Smith 9689* (AAS); same locality, Adélie Lake, 20 m, *Lewis Smith 9776* (AAS, KRAM); Cape King, 100–125 m, *Lewis Smith 10249* (AAS, KRAM).

Literature records. — BOUVETØYA: (Bell & Blom, 1986: 12; Engelskjøn & Jørgensen, 1986: 74; Engelskjøn, 1987: 145, 161 all as *C. exiliflora*; Ochyra & Váňa, 1989*b*: 215–216). SOUTH SANDWICH ISLANDS: Leskov Island (Grolle, 1972*a*: 83–84, partly as *Cephaloziella* sp.; Gimingham & Lewis Smith, 1970: 767; Fulford, 1976: 417 as *C. exiliflora*; Longton & Holdgate, 1979: 10, partly as *Cephaloziella* sp.; Ochyra & Váňa, 1989*b*: 216); Visokoi Island (Grolle, 1972*a*: 83–84 as *Cephaloziella* sp.; Gimingham & Lewis Smith, 1970: 767; Fulford, 1976: 417 as *C. exiliflora*; Longton & Holdgate, 1979: 10, partly as *Cephaloziella* sp.; Ochyra & Váňa, 1989*b*: 216); Candlemas Island (Longton, 1967: 228 as *Cephaloziella* sp.; Longton & Holdgate, 1967: 243 as *Cephaloziella* sp.; Grolle, 1972*a*: 83–84, partly as *Cephaloziella* sp.; Gimingham & Lewis Smith, 1970: 767; Fulford, 1976: 417 as *C. exiliflora*; Longton & Holdgate, 1979: 10, partly as *Cephaloziella* sp.; Ochyra & Váňa, 1989*b*: 216); Bellingshausen Island (Grolle, 1972*a*: 83–84, partly as *Cephaloziella* sp.; Gimingham & Lewis Smith, 1970: 767; Fulford, 1976: 417 as *C. exiliflora*; Longton & Holdgate, 1979: 10, partly as *Cephaloziella* sp.; Ochyra & Váňa, 1989*b*: 216). SOUTH ORKNEY ISLANDS: Without closer locality data (Fulford, 1976: 417 as *C. exiliflora*); Coronation Island (Ochyra & Váňa, 1989*b*: 216); Lynch Island (Bonner & Lewis Smith, 1985: 76, 82); Robertson Island (Ochyra & Váňa, 1989*b*: 216); Powell Island (Bonner & Lewis Smith, 1985: 91; Ochyra & Váňa, 1989*b*: 216); Signy Island (Longton & Holdgate, 1967: 248 as *Cephaloziella* sp.; Lewis Smith, 1972: 19, 28, 33, 37, 42, 45, 49, 52, 54, 62; 1985: 109; 1993: 63, 65 as *C. exiliflora*; Lewis Smith & Gimingham, 1976: 36; Fenton & Lewis Smith, 1982: 219; Ochyra & Váňa, 1989*b*: 216; Lewis Smith & Coupar, 1986: 194 as *C. exiliflora*; Davis, 1981: 126; 1986: 96). SOUTH SHETLAND ISLANDS: Elephant Island (Allison & Lewis Smith, 1973: 187, partly as *Cephaloziella* sp.; Lewis Smith 1979*a*: 235, parly as *Cephaloziella* sp.; Fenton & Lewis Smith, 1982: 219; Ochyra & Váňa, 1989*b*: 216); O'Brien Island (Lewis Smith, 1979*a*: 235; Ochyra & Váňa, 1989*b*: 216); King George Island (Lindsay, 1971: 75 as *Cephaloziella* sp.; Furmańczyk & Ochyra, 1982: 33; Ochyra *et al.*, 1982: 261 as *C.* cf. *exiliflora*; Ochyra, 1984: 12, 15, 21, 27; Ochyra *et al.*, 1986: 55; Ochyra & Váňa, 1989*a*: 198–199; 1989*b*: 216; Myrcha *et al.*, 1991: 163; Chen *et al.*, 1993: 50; 1995: 145–147 as *C. exiliflora*; Okada & Kanda, 1994: 58 as *C. exiliflora*; Seppelt & Green, 1998: 631–632 as *C. exiliflora*); Chen *et al.*, 1995: 145, 147; Li *et al.*, 1998*a*: 201; 1998*c*: 233 both as *C. exiliflora*); Robert Island (Bonner & Lewis Smith, 1985: 99); Livingston Island (Lindsay, 1971: 76 as *Cephaloziella* sp.; Bonner &

Lewis Smith, 1985: 155; Ochyra & Váňa, 1989*b*: 216; Sancho *et al.*, 1999: 322); Deception Island (Collins, 1969: 82; Lewis Smith, 1984*b*: 56; 1984*c*: 29, 31–32, 38, 47 both as *C.* cf. *exiliflora*; Ochyra & Váňa, 1989*b*: 216). WEST ANTARCTIC PENINSULA: Danco Coast (Stephani, 1901: 5; 1905: 334; Steere, 1961: 30; Fulford, 1976: 417 as *C. exiliflora*; Lewis Smith & Corner, 1973: 111, tab. VIII–X; Schuster & Damsholt, 1974: 325 as *C. arctica*; Schuster, 1980*a*: 148 as *C. arctica*; 1996*a*: 49; Bonner & Lewis Smith, 1985: 106; Ochyra and Váňa 1989*b*: 216); Graham Coast: Lewis Smith & Corner, 1973, tab. V; Fenton & Lewis Smith, 1982: 219; Bonner & Lewis Smith, 1985: 54; Ochyra & Váňa, 1989*b*: 216; Loubet Coast (Spaull, 1973: appendix as *Cephaloziella* sp.; Jennings, 1976: 81 as *Cephaloziella* sp.; Lewis Smith, 1995: 85 as *C.* cf. *exiliflora*; Lewis Smith & Convey, in press); Fallières Coast (Longton, 1967: 225; Duddington *et al.*, 1973: 88–89 both as *Cephaloziella* sp.; Spaull, 1973: table I, appendix as *Cephaloziella* sp.; Jennings, 1976: 83 as *Cephaloziella* sp.; Lewis Smith & Poncet, 1987: 34); George VI Sound (Lewis Smith, 1988*b*: 47; 1995: 85 as *C.* cf. *exiliflora*; Ochyra & Váňa, 1989*b*: 216; Convey *et al.*, 2000: 410; Lewis Smith & Convey, in press). EAST ANTARCTICA: Princess Elizabeth Land (Seppelt, 1983*a*: 28; 1983*b*: 4; 1984: 10; 1986: 238 as *C. exiliflora*; Lewis Smith & Poncet, 1987: 34; Seppelt & Green, 1998: 631–632 as *C. exiliflora*; Ochyra and Váňa 1989*b*: 216); Wilkes Land (Steere, 1965: 284; Greene, 1967: 11 both as *Cephaloziella* sp.; Seppelt, 1983*a*: 27; 1984: 10; Seppelt & Green, 1998: 631 all as *C. exiliflora*; Kanda, 1987: 77 as *C. exiliflora*; Lewis Smith, 1986: 86; 1988*a*: 156, 161; 1990*b*: 230, 234, 236–237, 241 all as *C. exiliflora*; Ochyra & Váňa, 1989*b*: 216; Hu & Seppelt, 1989: 322; Williams *et al.*, 1994: 34 both as *C. exiliflora*); Victoria Land (Greene, 1967: 11; Longton 1967: 233 both as *Cephaloziella* sp.; Bonner & Lewis Smith, 1985: 86; Lewis Smith & Poncet, 1987: 34; Kanda, 1987: 77; Broady *et al.*, 1987: 110 as *C. exiliflora*; Ochyra & Váňa, 1989*b*: 216; Williams *et al.*, 1994: 34; Seppelt & Green, 1998: 631–632 both as *C. exiliflora*; Green *et al.*, 1999: 500 as *C. exiliflora*).

CEPHALOZIELLACEAE SPECIES EXCLUDED FROM ANTARCTICA

Cephaloziella autoica R. M. Schust. — Schuster (1969*a*) reported this species as new to science from the Antarctic Peninsula region, but he did not provide any description of it. Thus, the status of this invalidly published species name remains unclear and it must be excluded from the present considerations.

Cephaloziella divaricata (Sm.) Schiffn. — Schuster (1971) stated that this species (reported as *C. byssacea* (Roth) Warnst.) “seems to be frequent on the Antarctic Peninsula (*RMS*; data to appear elsewhere)”. This information was in the context of discussion of the taxonomic status of *Cephaloziella dusenii* Steph., but it appears he was referring to what is here called *C. varians* (see above).

Cephaloziella exiliflora (Taylor) Douin. — If the taxonomic concept of the *C. exiliflora* complex is accepted, *C. exiliflora* itself has to be excluded from the Antarctic liverwort flora and all collections so-named should be referred to as *C. varians*.

Family V. ANTHELIACEAE R. M. SCHUST.

Antheliaceae R. M. Schust., J. Hattori Bot. Lab. **26**: 236. 1963. – TYPE: *Anthelia* (Dumort.) Dumort.

Plants very small, slender, prostrate to caespitose, terete and julaceous, isophyllous to slightly subisophyllous, whitish, greenish-blue to brownish. *Stem* simple, rather rigid, terminally (*Frullania*-type) or ventral-intercalary (*Bazzania*-type) branched, with weakly developed hyalodermis of thin-walled cells as large as the medullary cells, sometimes with 1–2 rows of intracortical, ± thick-walled cells (*Anthelia*) or with all cells thick-walled (*Grollea*). *Rhizoids* principally arising from underleaf bases or scattered over the ventral surface of the stem. *Leaves* contiguous to remote, transversely inserted, bifid to 0.5–0.8 of their length, with triangular, acute and entire-margined lobes; leaf cells oblong to quadrate, with ± thickened walls. *Underleaves* similar to and only slightly smaller than the lateral leaves. *Dioecious* or *paroecious*. *Androecia* intercalary on the main stem; male bracts similar to the lateral leaves, slightly concave, monandrous; antheridia with biseriate stalk; bracteoles without antheridia. *Gynoecia* terminal; female bracts and bracteoles similar to lateral leaves, but larger, closely imbricate, forming a terminal "head"-like structure. *Perianth* ovoid to obloid, deeply 3–6-plicate, contracted at the mouth. *Seta* with 16–24 outer and numerous inner cell rows. *Capsule* globose with bistratose wall; outer wall with nodular thickenings; inner wall with semiannular bands. *Spores* globose, 12–24 µm in diameter, finely papillose to verruculose; elaters 2–3-spiral; spore/elater width ratio 1.5–2.5 : 1.

A small family with only two genera, *Anthelia* and *Grollea*, and three species distributed in the cold and temperate regions of both Hemispheres. The monotypic genus *Grollea* is known only from southern South America (Schuster, 1972*b*; Hässel de Menendez, 1980*b*) and Schuster (1984, 2000) placed it in the own family Grolleaceae close to the Herbertaceae. A single species and genus of the Antheliaceae is known from the Antarctic.

1. ANTHELIA (DUMORT.) DUMORT.

Anthelia (Dumort.) Dumort., Recueil Observ. Jung.: 18. 1835. – *Jungermannia* L. sect. *Anthelia* Dumort., Sylloge Jung. Eur. Indig.: 63. 1831. – LECTOTYPE: *Anthelia julacea* (L.) Dumort. (*Jungermannia julacea* L.) (*fide* Spruce, 1882: 84; Müller, 1914: 315; Bonner, 1962: 163).

Plants small and slender, terete, isophyllous, greenish to brownish, secreting a water-repellent whitish substance. *Stem* creeping and closely prostrate or gregarious and forming caespitose patches or mats, simple or terminally branched, very rarely with ventral-intercalary branching, in transverse section with undifferentiated cortical (hyalodermis) and medullary cells or with 1–2 layers of subcortical cells with strongly thickened walls. *Leaves* transversely to slightly succubously inserted, ovate in outline, bilobed to 0.5–0.8 of their length; lobes lanceolate-triangular, acute, with margins entire or crenulate by projecting cells. *Underleaves* similar in size and shape to the lateral leaves or slightly smaller. *Leaf cells* thick-walled, without trigones; cuticle smooth or nearly so. *Gemmae* absent. *Dioecious* or *paroecious*. *Male bracts* similar to leaves, monandrous; antheridial stalk biseriate; bracteoles without antheridia. *Female inflorescence* with many deeply bifid female bracts. *Perianth* plicate, ovoid, lobed at the apex. *Seta* short, consisting of 16–24 epidermal cell rows surrounding many rows of inner cells. *Capsule* subglobose with bistratose walls. *Spores* minutely papillose to verruculose; elaters 2–3-spiral.

Anthelia is an isolated genus, comprising only two wide-ranging, principally arctic-alpine species, one of which is bipolar in range and is known from the northern maritime Antarctic. Schnyder (1988) considered this genus to be a monotype, consisting of only a single species, *A. julacea* (L.) Dumort., with two subspecies, but we do not accept this concept.

1. *Anthelia juratzkana* (LIMPR.) TREVIS. FIG. 42

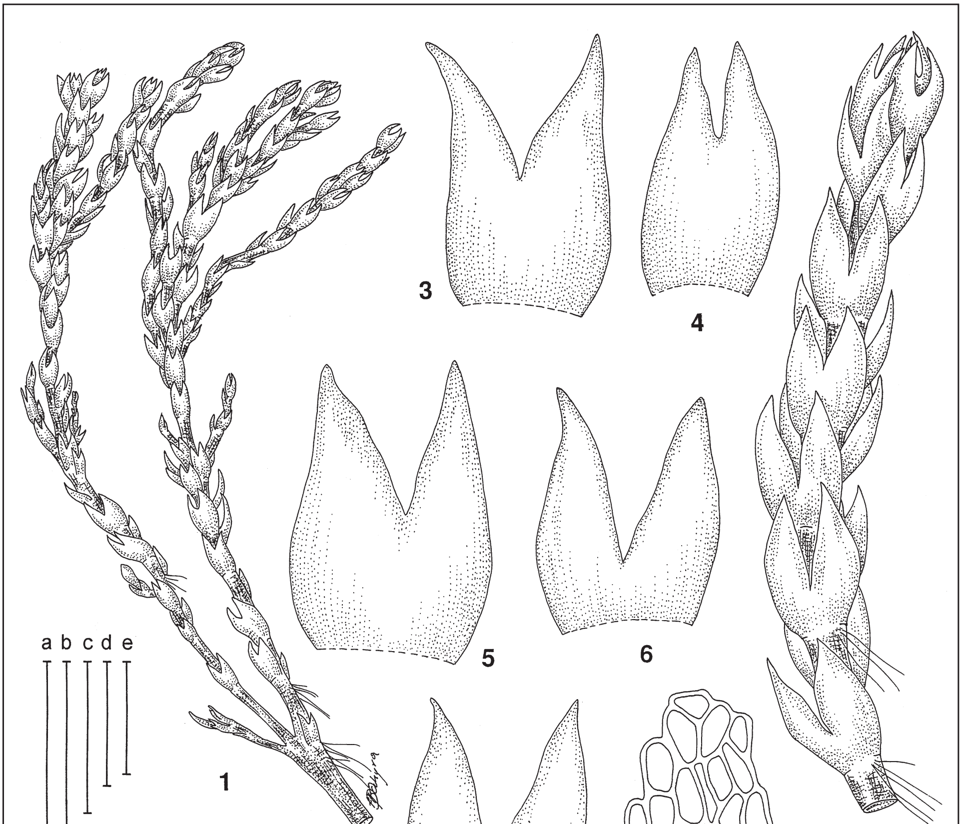
Anthelia juratzkana (Limpr.) Trevis., Mem. R. Ist. Lomb. Ser. 3, **4**: 416. 1877. – *Jungermannia juratzkana* Limpr. *in* Cohn, Krypt.-Fl. Schles. **1**: 289. 1876. – *Anthelia julacea* (L.) Dumort. subsp. *juratzkana* (Limpr.) Meyl., Beitr. Krypt. Fl. Schweiz **6**: 249. 1924. – TYPE: (1) [Czechia] Wurde von mir im Juli 1871 an der Südseite des Brunnesberges bei circa 1300 m. entdeckt; (2) ...durch den ganzen Alpenzug...; (3) citations of *Jungermannia julacea* [var.] γ *clavuligera* et γ* *glaucescens* Nees and *J. julacea* var. *nivalis* [LECTOTYPE (*fide* Schnyder, 1988: 57): "Bei der Furka im Wallis (Schweiz), 2225 m, 26.8.1871, leg. Jack" – BP-LIMPRICHT!].

Plants small, filiform to julaceous, usually prostrate or ascending in thin mats or scattered among other bryophytes, occasionally erect in short tufts, grey- or blue-green to silvery-grey. *Stems* (1–)3–10 mm long, 0.3–0.5 mm wide, simple or terminally branched, rarely with microphyllous stoloniform, ventral-intercalary branches, in transverse section consisting of hyalodermis of firm-walled cells, 16–25 μm wide, 1–2 rows of slightly smaller, thicker-walled, intracortical cells surrounding thin-walled medullary cells with small trigones of nearly the same size as the hyalodermis cells. *Rhizoids* mostly arising at bases of underleaves. *Leaves* nearly transversely inserted, contiguous to closely imbricate, appressed to the stem, ovate, bilobed to 0.5–0.7 of the length; lobes lanceolate-triangular, acute to acuminate with entire, not crenulate margins; leaf cells thin-walled to slightly thick-walled, quadrate to rectangular, 15–20 × 18–30 μm at the margin and 15–20 × 25–35 μm in mid-leaf; cuticle smooth. *Underleaves* similar to the lateral leaves, but somewhat smaller. *Sterile* in Antarctica.

Taxonomic and nomenclatural notes. — *Anthelia juratzkana* was described as *Jungermannia juratzkana* by Limpricht (1877) from material collected in Central Europe, mainly from the Sudetes and the Alps. The specimen collected by Jack in Switzerland was selected by Schnyder (1988) as lectotype. Although *A. juratzkana* is generally treated as a species in its own right, the distinction between it and *A. julacea* are extremely critical and sterile plants are almost impossible to separate. Therefore, in recent years several authors (Geissler, 1976; Grolle, 1976; Koponen *et al.*, 1977; Steere & Inoue, 1978) have doubted whether these two taxa merit the status of separate species, and Schnyder (1988) resurrected the old concept of Meylan (1924) and reduced *A. juratzkana* to a subspecies of *A. julacea*. In the present treatment, however, the traditional concept of *A. juratzkana* is accepted since this is the only representative of this genus in Antarctica and the correct naming of the plants do not pose any problems.

Differentiation. — *Anthelia juratzkana* is readily recognised in the field by its whitish or silvery, pale to bluish-green colour which is a result of secretation of a white, probably water-repellent substance covering the plants. Microscopically, the species is distinguished by its filiform and terete, isophyllous shoots with dense foliage of the imbricate and deeply bifid lateral leaves and underleaves.

Reproduction in Antarctica. — Fertile plants unknown.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Habitat. — On bare, permanently moist gravelly soil, on level or gently sloping ground and the margin of stone stripes, often below late snow patches; occasionally in moist shaded crevices. It is usually associated with *Bryum pseudotriquetrum*, *Cephaloziella varians*, *Conostomum magellanicum*, *Pachyglossa dissitifolia*, *Pohlia nutans* and *Warnstorfia sarmentosa*.

World range. — A bipolar species, widely distributed in the arctic-alpine regions of the Northern Hemisphere (Fig. 43, inset). Additionally, it is known from tropical high mountains in South America, East Africa (Ochyra & Pócs, 1992) and Malesia, reaching New Zealand, Tierra del Fuego, South Georgia[1] and Antarctica (Szweykowski, 1966; Grolle, 1969; Schuster, 1968*c*, 1969*c*, 1976, 1980*a*, 1983*a*; Váňa & Piippo, 1989).

Distribution in Antarctica. — A rather infrequent species in the South Orkney and South Shetland Islands, but locally abundant, extending as far south as lat. 62°40'S on Livingston Island (Fig. 44). Its altitudinal range extends from near sea level to about 250 m, but occurs on a nunatak on King George Island at 275 m.

Specimens examined. — SOUTH ORKNEY ISLANDS. **CORONATION ISLAND**. Cape Hansen, 25 m, *Lewis Smith 8690* (AAS, KRAM) and without elevation, *Lewis Smith 1856* (AAS, KRAM); Saunders Point, *ca* 15 m, *Lewis Smith 25B* (AAS, KRAM). **SIGNY ISLAND**. Moraine Valley, 30 m, *Lewis Smith 5206A* (AAS), *ca* 35 m, *Lewis Smith 659F* (AAS), 75 m, *Lewis Smith 10853* (AAS, KRAM), 100 m, *Lewis Smith 317A* (AAS, KRAM) and without elevation, *Lewis Smith 1836* (AAS, KRAM); west side of Rusty Bluff, 50 m, *Lewis Smith 541A* (AAS, KRAM); east side of Rusty Bluff above Paal Harbour, 100 m, *Lewis Smith 352A* (AAS, KRAM); above Paal Harbour, 75 m, *Lewis Smith 10864* (AAS, KRAM)

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[1] Schuster (1983*a*) incorrectly referred to the occurrence of *Anthelia juratzkana* on South Georgia. He misinterpreted the information of Greene (1964*b*) who actually mentioned this genus, without indication of the species, from the South Orkney Islands in the Antarctic botanical zone. So, until now this species has not been correctly reported from this subantarctic island. However, it was collected many times throughout the island and below some examples, preserved in AAS, are cited to substantiate the presence of *A. juratzkana* on South Georgia: **SOUTH GEORGIA**: south shore of Right Whale Bay, *ca* 10 m, *Clarke & Greene 32* (AAS); north-east corner of Antarctic Bay, *Collins 13* (AAS); eastern side of Church Bay, *Edwards 29B* (AAS); Bird Island, Gazella Peak, *ca* 165 m, *Greene 371E & 374D* (AAS); Hope Valley, *Greene 715D* (AAS); Bay of Isles, Paul Beach, northern peak of Murphy Wall, *ca* 335 m, *Greene 1258A* (AAS); about 0.25 mile inland from Husvik whaling station Stromness Bay, *Greene 1461A* (AAS); Prince Olav Harbour, North shore of North Bay, *ca* 85 m, *Greene 1689D* (AAS); Cumberland East Bay, north-west of Grytviken, to east of snout of Hodges Glacier, *ca* 415 m, *Greene 1813A* (AAS); Royal Bay, north-west shore of Moltke Harbour, *Greene 2120* (AAS); Royal Bay, corrie between Brocken and Mount Krokisius, *Greene 2367* (AAS); ridge between upper Husdal and Karakatta valleys, *ca* 200 m, *Lewis Smith 8334* (AAS).

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FIGURE 42. *Anthelia juratzkana*. **1–2**. Sterile plants. **3–5**. Leaves. **6–7**. Underleaves. **8**. Leaf cells. **9–10**. Cells at leaf apices. **11**. Transverse section of stem. (All from *Ochyra 158/80*, KRAM.) Scale bars: a – 1 mm (2); b – 0.5 mm (3–7); c – 100 µm (9–10); d – 100 µm (11); e – 1 mm (1) and 100 µm (8).

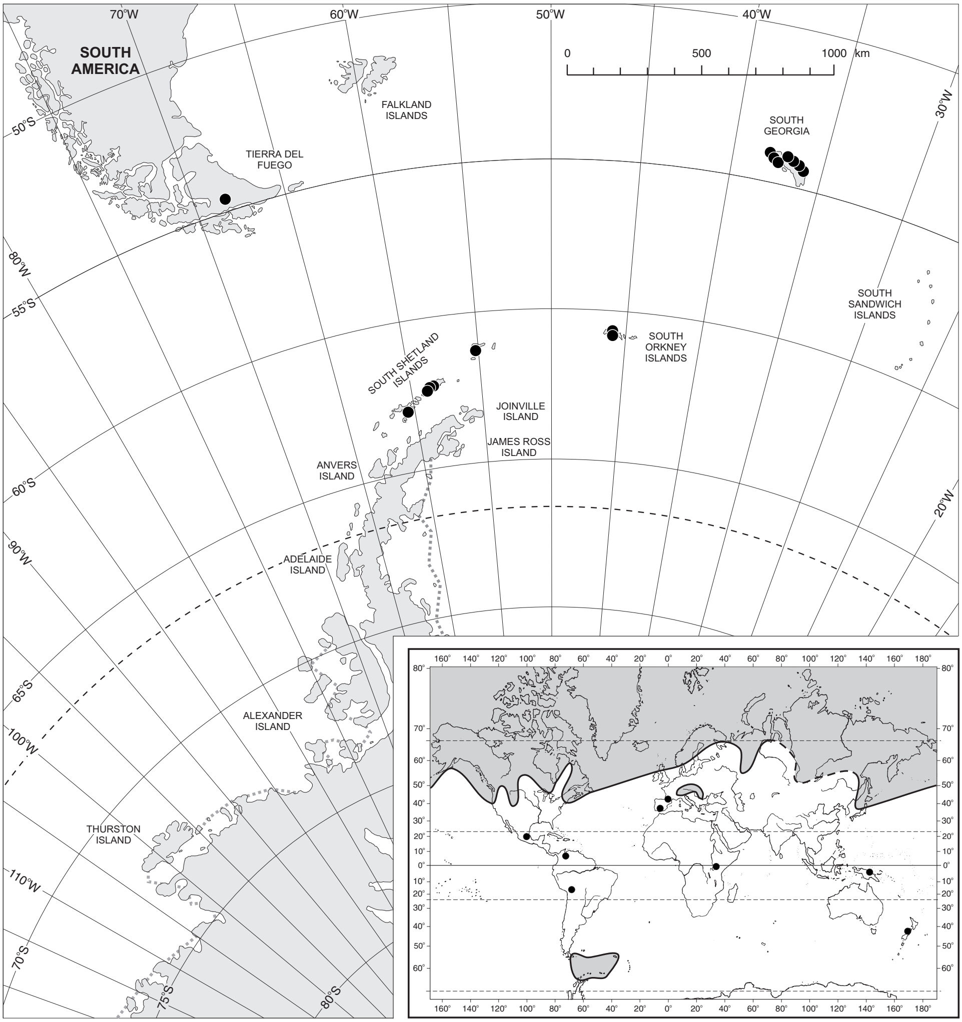

FIGURE 43. Distribution of *Anthelia juratzkana* in the Antarctic and Fuegian region. Inset: global distribution.

and *ca* 85 m, *Lewis Smith 681B, 682A & 683* (AAS, KRAM); Gneiss Hills, 200 m, *Lewis Smith 8111* (AAS).

SOUTH SHETLAND ISLANDS. **ELEPHANT ISLAND**. 2 km south-west of Endurance Glacier, 152 m, *Allison 28A* (AAS). **KING GEORGE ISLAND**. ***Bransfield Strait***: Red Hill, 120–130 m, *Ochyra 1087/80 & 1090/80* (KRAM, PRC). ***Admiralty Bay***: Sphinx Hill, 100 m, *Ochyra 272/80* (KRAM, PRC); Hala, 20 m, *Ochyra 2385/80* (KRAM, PRC); Ubocz, 90 m, *Ochyra 2361/80* (KRAM, PRC); Jardine Peak, 275 m, *Ochyra 5166/79* (AAS, KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 47]; unnamed hills on Wróbel Glacier, 150 m, *Ochyra 158/80* (KRAM, PRC); Italia Valley 100 m, *Ochyra 113/80*

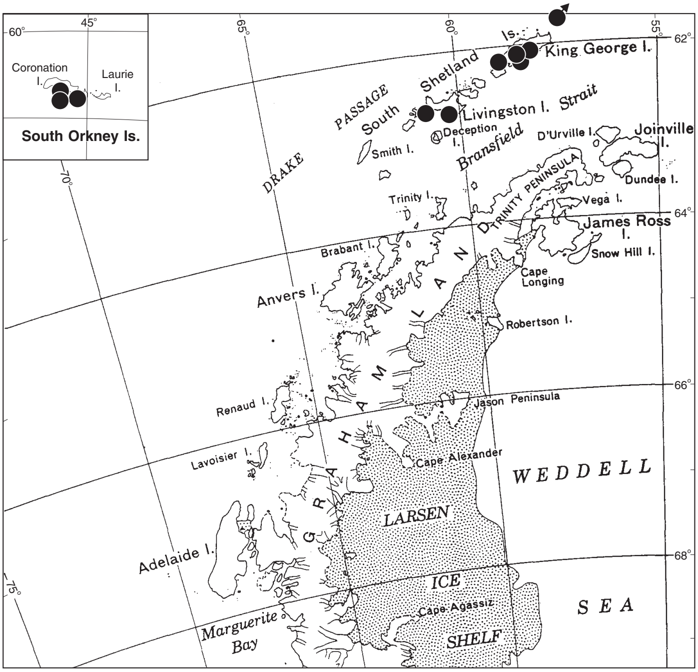

FIGURE 44. Distribution of *Anthelia juratzkana* in the Antarctic. The locality on Elephant Island is indicated by an arrow.

(KRAM, PRC) and 200 m, *Ochyra 59/80* (KRAM, PRC); Mt. Wawel, 20 m, *Ochyra 2189/80* (KRAM, PRC). ***Fildes Peninsula***: without specific locality, *Nikolaev s.n.* (LE, PRC). LIVINGSTON ISLAND. ***Byers Peninsula***: between Chester Cone and Sealers Hill, *Lewis Smith 3823* (AAS, KRAM). ***Hurd Peninsula***: South Bay, 110 m, *Schulz 68* (Hb. Schulz, KRAM).

Literature records. — SOUTH ORKNEY ISLANDS: without indication of the island (Greene, 1964*b*: 178); Signy Island (Lewis Smith, 1972: 19, 28, 37; Lewis Smith & Gimingham, 1976: 36 both as *Anthelia* sp.; Ochyra & Váňa, 1989*b*: 216). SOUTH SHETLAND ISLANDS: Elephant Island (Allison & Lewis Smith, 1973: 187; Lewis Smith, 1979*a*: 235; Ochyra & Váňa, 1989*b*: 216); King George Island (Ochyra, 1984: 8; Ochyra *et al*., 1986: 55; Ochyra & Váňa, 1989*a*: 200; 1989*b*: 216); Livingston Island (Schuster, 1969*a*: 103; 1974: 634; 2000: 172; Schuster & Damsholt, 1974: 282: (Bonner & Lewis Smith, 1985: 155); Ochyra & Váňa, 1989*b*: 216; Sancho *et al*., 1999: 321).

Family **VI. LOPHOZIACEAE** CAVERS

Lophoziaceae Cavers, New Phytol. **9**: 293. 1910. – TYPE: *Lophozia* (Dumort.) Dumort.

Plants very small to large, anisophyllous to subisophyllous, green, yellowish-green to brownish, sometimes with reddish pigmentation. *Stems* creeping, prostrate to erect, simple or terminally (*Frullania*-type), lateral-intercalary (*Plagiochila*-type and *Anomoclada*-type) or rarely also ventral-intercalary (*Bazzania*-type) branched, mostly opaque, soft-textured, with 1(–2)-stratose cortex scarcely differentiated from medulla, or often ± rigid with a multistratose cortex of ± thick-walled cells. *Rhizoids* scattered over the ventral surface of the stem, hyaline. *Leaves* succubously to nearly transversely inserted, unlobed to frequently 2—4-lobed, with a tendency to develop cilia near the base, entire-margined or often ± sinuate; leaf cells mostly thick- to thin-walled with large or without trigones; cuticle smooth or papillose-striate. *Underleaves* absent, rudimentary or well developed, usually much smaller than lateral leaves, free, appressed or elevated and incurved, lanceolate, unlobed to bilobed or bifid, entire or ciliate at margins. *Gemmae* relatively common on modified or unmodified leafy shoots, oval to stellate, mostly 2-celled, green or pigmented. *Dioecious*, *paroecious*, very rarely *autoecious*. *Male inflorescences* terminal to intercalary; male bracts saccate, usually subequal to the leaves, often with one additonal teeth, comprising 1–4 antheridia on 1–2-seriate stalks. *Female inflorescence* terminal; female bracts erect or spreading, mostly lobed or at least laciniate at margins. *Perianth* ovoid to cylindrical, contracted at the mouth, 4–5(–10)-plicate at least above. *Seta* unspecialised or reduced to 8 outer and 4 inner cell rows. *Capsule* ovoid, ellipsoidal to subglobose, with 2–5-layered wall; epidermal cells with nodular thickenings; inner cells with semiannular thickenings. *Spores* globose, smooth to papilose; spore/elater width ratio mostly 2 : 1.

The Lophoziaceae are closely related to the Jungermanniaceae and these families have been variously delimited and circumscribed. Schuster (1969*b*) initially followed the traditional delimitation of these families as outlined by Jørgensen (1934) and Müller (1939–1940) which separated the Lophoziaceae on account of the 2–4-lobed leaves and 2–5-stratose capsule wall (in contrast to undivided or merely retuse leaves and bistratose capsule wall in the Jungermanniaceae *s. str.*). Later Schuster (1970) merged both families into a single large family, Jungermanniaceae, which was subsequently subdivided into nine subfamilies. This concept was accepted with some minor modifications by Grolle (1972*b*, 1983*a*), Váňa (1973) and Schuster (1979*a*, 1984). However, some authors (e.g. Steere & Inoue, 1975, 1978; Schljakov, 1980, 1981; Grolle, 1983*b*; Paton, 1999) did not accept the broad concept of the family Jungermanniaceae and continued to use, sometimes for strictly practical reasons, the traditional narrower concept of this family to exclude it from the Lophoziaceae.

In the present treatment the traditional circumscription of the Lophoziaceae is adopted, largely following the concept presented by Váňa and Inoue (1983) and recently developed by Váňa (1999). These authors divided this family into four subfamilies, namely Lophozioideae, Jamesonielloideae (which traditionally was placed in the Jungermanniaceae), Gottschelloideae and Nothostreptoideae. In the present circumscription the Lophoziaceae comprise 28 genera with 224 species. Of these, 16 or 17 genera (the position of *Rhodoplagiochila* is uncertain) with about 175 species belong to the type subfamily, seven genera with 45 species to the Jamesonielloideae and one genus and two species to each of the last two subfamilies Gottschielloideae and Nothostreptoideae. Four genera and five species are present in the Antarctic. They belong within two subfamilies, namely the Lophozioideae (*Barbilophozia*, *Lophozia* and *Roivainenia*) and the Jamesonielloideae (*Cryptochila*), and are recognised in the key below.

KEY TO THE ANTARCTIC GENERA OF THE LOPHOZIACEAE

1. Leaves unlobed .... **2. *Cryptochila***
1. Leaves 2–4-lobed 2
   2. Leaves 3–4-lobed .... **1. *Barbilophozia***
   2. Leaves 2(–3)-lobed 3
3. Plants greenish; cuticle nearly smooth; underleaves absent .... **3. *Lophozia***
3. Plants yellowish-brown to brownish; cuticle coarsely papillose; underleaves present .... **4. *Roivainenia***

1. BARBILOPHOZIA LOESKE

Barbilophozia Loeske, Verh. Bot. Ver. Prov. Brandenburg **49**: 37. 1907. – LECTOTYPE: *Barbilophozia barbata* (Schmid. *ex* Schreb.) Loeske (*Jungermannia barbata* Schmid. *ex* Schreb.) (*fide* Schuster, 1969*b*: 334).

Plants small, medium-sized to large and robust, in large, thin mats, green, yellowish-green or brownish, rarely reddish. *Stems* rigid and firm, prostrate to ascending or erect, simple to rarely terminally (*Frullania*-type) to lateral-intercalary (*Plagiochila*-type) branched, in transverse section consisting of 1–2(–3)-stratose cortex of ± smaller, thick-walled cells surrounding medulla of large and thin-walled cells. *Rhizoids* relatively rare, dispersed on the ventral side of the stem and forming a dense tomentum concealing underleaves. *Leaves* succubously to subtransversely inserted, quadrate to transversely obrhombic or reniform-obtrapezoidal, broader than long, nearly symmetrical, with postical leaf bases armed with 1 to several flexuose cilia, 2–4-lobed; lobes broadly ovate-triangular, rounded or acute at the apex; leaf cells thin-walled to slightly thick-walled, mostly with large to nodulose trigones; cuticle smooth to verruculose. *Underleaves* present or less often absent, small, typically deeply bifid, with subulate lobes and ciliate margins, lanceolate and bilobed. *Gemmae* present on modified or weakly specialised shoots or absent. *Dioecious*. *Male bracts* saccate, with 2–several antheridia. *Female bracts* sometimes with supplementary lobes or teeth, more or less connate with bracteoles. *Perianth* cylindrical, plicate, contracted at the mouth; mouth somewhat lobed and dentate or dentate-ciliate.

Barbilophozia is not universally recognised as a separate genus and some authors consider it merely as a subgenus of the large and all-encompassing genus *Lophozia*. Whatever taxonomic rank is accepted, this taxon is distinct and easily distinguished by its tri- or quadrilobed leaves which are widest at or above the middle, have equal or subequal lobes, and the bases of the ventral margins possess one or more cilia composed mostly of elongate cells. *Barbilophozia* is a medium-sized genus consisting of 12 species, mostly with Holarctic distribution (only *Lophozia anomala* is known from Chile). It is divided into two subgenera, subgen. *Orthocaulis* and subgen. *Barbilophozia* comprising eight and four species, respectively. One bipolar species is known to occur in the Antarctic.

1. ***Barbilophozia hatcheri*** (A. Evans) Loeske FIG. 45

Barbilophozia hatcheri (A. Evans) Loeske, Verh. Bot. Ver. Prov. Brandenburg **49**: 37. 1907. – *Jungermannia hatcheri* A. Evans, Bull. Torrey Bot. Cl. **25**: 417. 1898. – *Lophozia hatcheri* (A. Evans) Steph., Résult. Voy. S. Y. Belgica 1897–1899 Rap. Sci. **6**(5): 4. 1901. – *Barbilophozia lycopodioides* (Wallr.) Loeske var. *hatcheri* (A. Evans) Schljakov, Pechon. Mkhi Sev. SSSR **3**: 32. 1980. – TYPE: Lapotaia [sic!]; also South Georgia [the specimen reported by Gottsche (1890) as *Jungermannia barbata* B. *Flörkii*] Dr Will Nr. 35

(im obersten Rasen). Süd-Georgien, Bachgrund oberhalb der Pinguinbay; 26. Januar 1883 [SYNTYPES: (1) Argentina, Terr. Tierra del Fuego, Lapataia, *J. B. Hatcher 35b* – NY (*fide* Engel, 1990*a*: 96; *non vidi*); (2) "№ 35 varia. Jungermannia barbata Flörkii Orig. Gottsche Bachgrund oberhalb der Pinguinbay. Süd-Georgien. 26/I.83" (leg. Dr. Will on the outside label) – M!].

Plants small to medium-sized, 2–5 cm long, 0.8–2.5 mm wide, in thin to deep mats or in loose tufts, green, greyish, yellowish, pale yellowish-brown to reddish-green or brown. *Stems* prostrate or ascending to erect, simple or rarely lateral-intercalary branched, in transverse section with 1–2-layered cortex, usually more prominent dorsally, of thick-walled cells, 15–22 µm wide, surrounding thin-walled, larger, 25–35 µm wide, not or rarely mycorrhizal medullary cells. *Rhizoids* dense, relatively short. *Leaves* very obliquely succubously inserted, spreading or erecto-patent, slightly undulate, concave or nearly flat, asymmetrical, quadrate to obrhomboidal, invariably 3–4-lobed to 0.2–0.4 of the length, postical base with 2–3 long cilia composed of elongate cells; lobes ovate-triangular, relatively wide, apiculate, sinuses acute, slightly gibbous; leaf cells subquadrate to subhexagonal, thin-walled, with small to large trigones, 15–25 × 25–30 µm. *Underleaves* large, bifid to 0.7–0.8 their length, with very narow lobes, ciliate at base. *Gemmae* abundant at margins of upper leaves and underleaves, reddish-brown, polygonal to ovate, bicellular, 20–25 µm wide. *Remainder* unknown.

Taxonomic and nomenclatural notes. — This is one of only a few bryophyte species which has a widespread Holarctic distribution, but was first named from material from the Southern Hemisphere. Other examples include *Cephaloziella varians* among liverworts, and *Sphagnum magellanicum* Brid. and *S. fimbriatum* Wils. amongst mosses. *Barbilophozia hatcheri* was first recognised in Europe as a separate species by Massolongo (1895) but the name proposed by this author, *Jungermannia collaris*, proved to be an earlier homonym of *J. collaris* Nees which is now applied to a widespread species of *Lophozia*. Ten years earlier Schiffner and Schmidt (1886) distinguished this species as a separate taxon when describing *Jungermannia barbata* var. *pusilla* from Bohemia.

Although at present *Barbilophozia hatcheri* has some additional heterotypic synonyms from Europe, the South American epithet has to be used. It was introduced by Evans (1898, 1903) and honoured J. B. Hatcher, who first collected this plant. He was a geologist and member of the Princeton University Expedition to Patagonia in 1896–1897 and collected this new species in Bahía Lapataia (in the paper incorrectly given as "Lapotaia") east of Ushuaia in the Argentine part of Isla Grande de Tierra del Fuego. Apart from the specimen collected by Hatcher, Evans (1898) cited in the protologue the plants collected by H. Will on South Georgia during the German International Polar-Year Expedition of 1882–1883. They were reported by Gottsche (1890) as *B. floerkei* (F. Weber & D. Mohr) Loeske. Thus,

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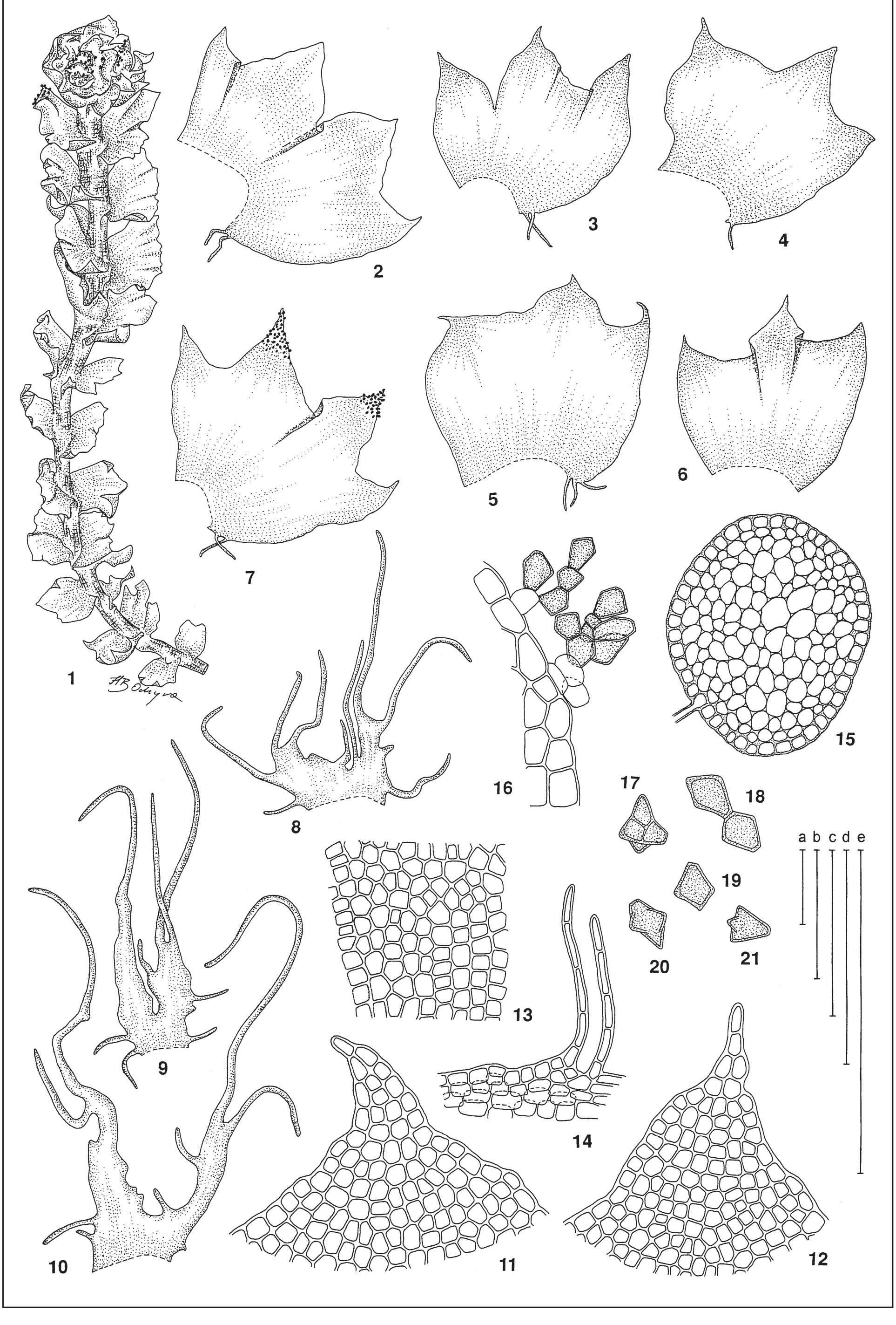
FIGURE 45. *Barbilophozia hatcheri*. **1**. Sterile shoot, dorsal view. **2–6**. Leaves. **7**. Gemmiferous leaf. **8–10**. Underleaves. **11–12**. Lobe apices. **13**. Mid-leaf cells. **14**. Cilia from base of leaf. **15**. Transverse section of stem. **16**. Gemmiferous leaf lobe. **17–21**. Gemmae. (All from *Lewis Smith 459*, AAS.) Scale bars: a – 50 µm (16) and 100 µm (11–15); b – 1 mm (2–7); c – 100 µm (17–21); d – 5 mm (1); e – 1 mm (8–10).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correctly, a lectotypification is necessary, but only the specimen from South Georgia deposited in M was available for us during the present study. All early collections of *B. hatcheri* from the Southern Hemisphere, including Antarctica, were misnamed as *B. floerkei*, but the source of confusion between these two species was clarified by Grolle (1960*a*).

Barbilophozia hatcheri is closely related to *B. lycopodioides* and both species can be safely separated only by considering a set of characters, mostly referring to the aspect of the leaves. They are generally considered as separate species, but Schljakov (1973, 1980) reduced *B. hatcheri* to a variety of *B. lycopodioides*. However, the epithet *pusilla* should be used at varietal level, not *hatcheri* as proposed by Schljakov (1973, 1980), because it is the oldest one available for this taxon in varietal rank. In the Antarctic this species does not pose any problems with identification and therefore the species status is accepted for it.

Differentiation. — A very characteristic species, usually easily recognised from all other Antarctic hepatics by its mostly quadrilobed leaves. However, trilobed leaves are not uncommon and may be confused with *Lophozia excisa* in which trilobed leaves may be occasionally found, but in the latter species underleaves are absent.

Reproduction in Antarctica. — Fertile plants unknown, but gemmae are commonly produced.

Habitat. — On soil and gravelly ground and rocks, usually in protected habitats on wind-swept scree, in damp and sheltered rock crevices and fissures, under overhangs, on narrow ledges, and on sheltered hillsides. The species usually grows as dense green or reddish-brown patches intermixed with mosses on *Chorisodontium aciphyllum* and *Polytrichum strictum* turf banks, as well as with *Andreaea depressinervis*, *A. gainii* and *A. regularis*, *Polytrichastrum alpinum* and *Polytrichum juniperinum* in various communities of the fruticose lichen and moss cushion subformation.

World range. — A bipolar species having a wide, arctic-subalpine distribution in the Holarctic (Szweykowski & Koźlicka, 1980*a*) and in the Southern Hemisphere known from the southernmost tip of South America and South Georgia, the Falkland Islands (Engel, 1990*a*) and Antarctica (Fig. 46).

Distribution in Antarctica. — A frequent and widely distributed species in the maritime Antarctic, extending from the South Orkney Islands south to the Fallières Coast, reaching its southernmost locality on Adelaide Island in northern Marguerite Bay at lat. 67°34'S (Fig. 47).

Specimens examined. — SOUTH ORKNEY ISLANDS. CORONATION ISLAND. Mansfield Point, *ca* 15 m, *Lewis Smith 147A* (AAS, KRAM) *& 298B* (AAS); Cape Vik, 100 m, *Lewis Smith 573E* (AAS); Cape Hansen, 5–30 m, *Lewis Smith 3239* (AAS, KRAM); below Windscoop Buttress on east side of Sunshine Glacier, *ca* 175 m, *Webb 152B* (AAS, KRAM); Olivine Point, *ca* 35 m, *Lewis Smith 147A* (AAS, KRAM); Saunders Point, *ca* 35 m,

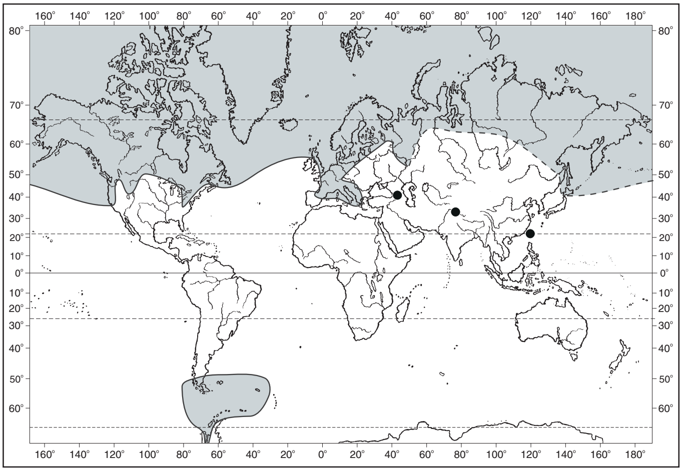

FIGURE 46. Global distribution of *Barbilophozia hatcheri*.

Lewis Smith 18A (AAS, KRAM). **LYNCH ISLAND**. Alt. *ca* 15 m, *Lindsay 954B, 955B, 956B, 987B & 989* (AAS, KRAM). **MATTHEWS ISLAND**. Near The Divide on north-east coast, 100 m, *Lewis Smith 178A* (AAS, KRAM); promontory north of Coffer Island, *ca* 35 m, *Lewis Smith 186* (AAS, KRAM); north-east peninsula, 6–20 m, *McManmon 104* (AAS, KRAM). **POWELL ISLAND**. Above north-west coast, 300 m, *Lewis Smith 240A* (AAS, KRAM) *& 241C* (AAS); promontory to west of John Peaks, *ca* 35 m, *Lewis Smith 248B & 259* (AAS,

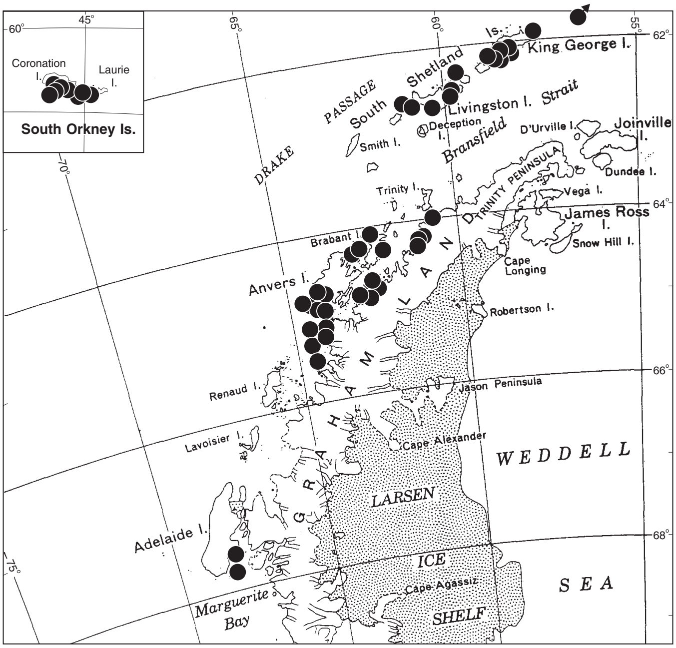

FIGURE 47. Distribution of *Barbilophozia hatcheri* in the Antarctic. The localities on Elephant and Clarence Islands are indicated by an arrow.

KRAM); south-east coast, *ca* 135 m, *Lewis Smith 194B* (AAS, KRAM); middle of east coast, *ca* 135 m, *Lewis Smith 220A* (AAS, KRAM). **Christoffersen Island**. Southern end, 50 m, *Richard 172B* (AAS, KRAM). **Laurie Island**. Scotia Bay, 50 m, Dec 1962, *Bellisio s.n.* (BA); Martin Point, 25 m, Dec 1962, *Bellisio s.n.* (BA) and 1000 m, Dec. 1963, *Bellisio s.n.* (BA) and without altitude, 27 Dec 1952, *Kühnemann s.n.* (BA); Point Davis, 6–30 m, *McManmon 125* (AAS, KRAM). **Signy Island**. Port Jebsen, *ca* 15 m, *Holdgate 770A* (AAS, KRAM); Foca Point, *ca* 35 m, *Longton 1114* (AAS, KRAM); Knife Point, 20 m, *Lewis Smith 5215* (AAS, KRAM), *ca* 25 m, *Lewis Smith 486A* (AAS, KRAM) and without elevation, *Lewis Smith 1847 & 1855* (AAS, KRAM); south-east shore of Factory Cove, 50 m, *Longton 1166B & 1167* (AAS, KRAM); Factory Cove, behind base, *Lewis Smith 1849* (AAS, KRAM); south shore of Factory Cove, 50 m, *Lewis Smith 40A* (AAS, KRAM); slope above Factory Cove, 70 m, *Lewis Smith 5200* (AAS, KRAM), 85 m, *Lewis Smith 5207, 5211 & 5213* (AAS) and 100 m, *Lewis Smith 5209, 5210 & 5212* (AAS); overlooking Factory Cove, *ca* 15 m, *Taylor 378* (AAS, KRAM); between Factory Cove and Paal Harbour, *ca* 65 m, *Longton 1079* (AAS, KRAM); Berntsen Point, *ca* 35 m, *Taylor 359* (AAS, KRAM); north side of Observation Bluff, 25 m, *Holdgate 70* (AAS, KRAM), 50 m, *Lewis Smith 692B* (AAS, KRAM) and 65 m, *Lewis Smith 115B* (AAS, KRAM) and *Holdgate 109B* (AAS, KRAM); Polynesia Point, 50 m, *Lewis Smith 10743* (AAS, KRAM); Moraine Valley, 50 m, *Longton 1081* (AAS, KRAM), 65 m, *Lewis Smith 5205A* (AAS, KRAM), 75 m, *Lewis Smith 10849* (AAS, KRAM) and 100 m, *Lewis Smith 10848* (AAS, KRAM); Paal Harbour, *ca* 35 m, *Holdgate 751C* (AAS, KRAM); cliffs above Paal Harbour on Rusty Bluff, 80 m, *Lewis Smith 5193B* (AAS, KRAM) and without elevation, *Lewis Smith 1845 & 1846* (AAS, KRAM); east side of Rusty Bluff above Paal Harbour, *ca* 135 m, *Lewis Smith 459* (AAS, KRAM); near Rusty Bluff, *ca* 135 m, *Taylor 400* (AAS, KRAM); Tilbrook Hill, 50 m, *Longton 1152* (AAS, KRAM). **Moe Island**. 10–200 m, *Lewis Smith 5256* (AAS).

SOUTH SHETLAND ISLANDS. **Elephant Island**. 2 km south-west of Endurance Glacier, 152 m, *Allison 32C* (AAS) and 167 m, *Allison 22D* (AAS); 0.5 km south-west of Endurance Glacier, 183 m, *Allison 152A* (AAS) and 244 m, *Allison 179E* (AAS); 0.5 km south of Stinker Point, 122 m, *Allison 92B* (AAS); 3 km south-west of Walker Point, 153 m, *Allison 185* (AAS). **Clarence Island**. South end, 152 m, *Allison 1K* (AAS). **King George Island**. ***Admiralty Bay***: Demay Point, 55 m, *Ochyra 1359/80* (AAS, KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 21]; Creeping Slopes, 90 m, *Ochyra 1246/80* (AAS, KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 149]; Ubocz, 125 m, *Ochyra 2360/80* (KRAM, PRC); Jersak Hills, 180 m, *Ochyra 5148/79* (KRAM, PRC); Komandor Peak, 250 m, *Ochyra 1937/80* (KRAM, PRC) *& 1941/80* (AAS, KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 49]; Admiralen Peak, 305 m, *Ochyra 2026A/80* (KRAM, PRC); Shark Fin, 140 m, *Ochyra 2655/80* (KRAM, PRC); Ullman Spur, 40 m, *Ochyra 592/80* (KRAM, PRC) and 60 m, *Ochyra 595/80* (KRAM, PRC); Mt. Wawel, 40 m, *Ochyra 2134/80* (KRAM, PRC) *& 2140/80* (AAS, KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 48] and 70 m, *Ochyra 2165/80* (KRAM, PRC); Basalt Point, 15 m, *Ochyra 2222/80* (KRAM, PRC). ***Barton Peninsula***: Winship Point, 5 m, *Jabłoński 193* (KRAM). ***Fildes Peninsula***: Ardley Island, *Kühnemann 25, 38 & 42* (AAS, KRAM) and *Nikolaev 2, 8 & 82* (LE, PRC); Bukhta Gidrografov, *Nikolaev 76* (LE, PRC). ***Destruction Bay***: Faraway Nunatak, *Jabłoński 173* (KRAM). **Robert Island**. Coppermine Cove, 15–25 m, *Lewis Smith 928* (AAS, KRAM). **Greenich Island**. Discovery Bay, Spark Point, 20 m, *Lindsay 631B*

(AAS, KRAM). **Half Moon Island**. Hill south of Huts, 50 m, *Lindsay 587* (AAS, KRAM). **Livingston Island**: ***Byers Peninsula***: West Beach, between Smellie Point and Devils Point, 5 m, *Richard 28A & 29B* (AAS, KRAM); Ocoa Point, 20–75 m, *Richard 28A* (AAS, KRAM); between Chester Cove and Sealers Hill, 25–30 m, *Lewis Smith 3822* (AAS, KRAM); extreme end of South Beaches, 6 m, *Lindsay 92* (AAS) and 17 m, *Lindsay 426* (AAS); Vietor Rock, *Lindsay 458* (AAS). ***Hurd Peninsula***: South Bay, 25 m, *Schulz 78* (Hb. Schulz, KRAM).

WEST ANTARCTIC PENINSULA. **Davis Coast**. Cape Andreas, 29 Nov 1902, *Skottsberg s.n.* (G, S). **Danco Coast**. Cierva Point, *Komárková 491, 590, 619 & 627* (KRAM); Moss Island, 1 Dec 1902, *Skottsberg 397* (G, S); Spring Point, *Komárková 1192, 1203, 1204, 1223, 1259 & 1279* (KRAM); Centre Rocks, 7 Feb 1952, *Hässel de Menendez s.n.* (BA); Cuverville Island, *Racovitza 243B & 243C* (BR, G), 10–50 m, *Lewis Smith 4212* (AAS, KRAM), *ca* 20 m, *de Leeuw 12* (AAS, KRAM), 25 m, *de Leeuw 13A* (AAS, KRAM) and 40 m, *Lewis Smith 8811* (AAS, KRAM); Birdsend Bluff, 5–35 m, *Lewis Smith 4225* (AAS, KRAM); Andvord Bay, Neko Harbour, 10 Feb 2000, *Kuc s.n.* (Hb. Kuc); Paradise Harbour, 7 Jan 1984, *Birkenmajer s.n.* (KRAM); Coughtrey Peninsula, Almirante Brown Station, 17 Dec 1954, *Kühnemann s.n.* (BA). ***Brabant Island***: without closer locality data, *Racovitza 252F, 252G & 252H* (BR, G) and *Hankinson 189B* (AAS, KRAM); Hunt Island, *ca* 135 m, *Moffat 51* (AAS, KRAM); islet to west of Metchnikoff Point, 30 m, *Moffat 61B* (AAS, KRAM); "Easter Island" north-east of Metschnikoff Island, 50 m, *Moffat 76B* (AAS, KRAM). ***Melchior Islands***: Omega Island, Canal Murature, 20–25 m, *Frolick 10* (AAS, KRAM); Gamma Island, 5–10 m, *Lewis Smith 4153* (AAS, KRAM). ***Joubin Islands***: small island near the middle of the archipelago, 5–10 m, *Lewis Smith 1998* (AAS, KRAM); largest island of the archipelago, 20–50 m, *Lewis Smith 1990* (AAS, KRAM). ***Anvers Island***: Bonaparte Point, *Komárková 47A & 1166* (KRAM); Cape Monaco, *Komárková 745* (KRAM); Dream Island, *Komárková 993* (KRAM); Litchfield Island, 10 m, *Corner 360B, 366B & 373* (AAS, KRAM) and *ca* 15 m, *Corner 389* (AAS, KRAM); Hermit Island, 15–25 m, *Lewis Smith 887* (AAS, KRAM); Shortcut Island, *Komárková 1117* (KRAM); Laggard Island, *ca* 15 m, *Longton 1296* (AAS, KRAM). **Graham Coast**. Rasmussen Island, 19 m, *Scott 76C* (AAS, KRAM) and *Lewis Smith 1926* (AAS, KRAM); Edge Hill, *ca* 35 m, *Corner 656B* (AAS, KRAM); Cape Tuxen, *Archibald 21 & 29* (AAS, KRAM) and *ca* 65 m, *Corner 850CC* (AAS, KRAM). ***Peterman Island***: 50 m, *Scott 130B* (AAS, KRAM), 60 m, *Scott 123B & 125B* (AAS, KRAM), 71 m, *Scott 114B* (AAS, KRAM) and 89 m, *Scott 134B* (AAS, KRAM). ***Argentine Islands***: Galindez Island, *ca* 15 m, *Longton 1255 & 1256* (AAS, KRAM) and *ca* 25 m, *Corner 417B* (AAS, KRAM); same island, overlooking Meek Channel, *ca* 6 m, *Corner 449* (AAS, KRAM) and *Taylor 62, 68 & 72* (AAS, KRAM); same island, Stella Creek, 10 m, *Corner 441A* (AAS, KRAM) and *ca* 25 m, *Corner 412* (AAS, KRAM); same island, north-east slopes of Woozle Hill, *Taylor 92A & 95A* (AAS, KRAM); Irizar Island, east side, 10 m, *Corner 607* (AAS, KRAM); north-east side of Uruguay Island, 10–25 m, *Lewis Smith 4274 & 4275* (AAS, KRAM). ***Grandidier Channel***: Leroux Bay, west side of Lahille Island, 2–5 m, *Lewis Smith 4329A* (AAS, KRAM); largest island off Takaki Point, 10–35 m, *Lewis Smith 434* (AAS, KRAM); Takaki Point, 5–20 m, *Lewis Smith 4391* (AAS, KRAM). **Loubet Coast**. Lagoon Island, 35 m, *Lewis Smith 269/98* (AAS, KRAM). **Fallières Coast**. Adelaide Island, Rothera Point, 25 m, *Fenton 52B* (AAS, KRAM).

Literature records. — SOUTH ORKNEY ISLANDS: Lynch Island (Bonner & Lewis Smith, 1985: 82); Powell Island (Bonner & Lewis Smith, 1985: 91); Signy Island (Lewis Smith, 1972: 19, 28, 45, 49, 52, 62; 1978: 897; Lewis Smith & Gimingham, 1976: 36; Fenton & Lewis Smith, 1982: 219; 1987: 240; Lewis Smith & Coupar, 1986: 194; Ochyra & Váňa, 1989*b*: 216). SOUTH SHETLAND ISLANDS: Elephant Island (Allison & Lewis Smith, 1973: 187; Lewis Smith, 1979*a*: 235; Fenton & Lewis Smith, 1982: 219; Ochyra & Váňa, 1989*b*: 216); Clarence Island (Lewis Smith, 1979*a*: 235; Ochyra & Váňa, 1989*b*: 216); King George Island (Lindsay, 1971: 75 as *Barbilophozia* sp.; Ochyra *et al*., 1982: 261; 1986: 55; Ochyra, 1984: 5, 8–9, 21; Ochyra & Váňa, 1989*a*: 201; 1989*b*: 216; Myrcha *et al.*, 1991: 163; Chen *et al*., 1993: 50; 1995: 132–134; Okada & Kanda, 1994: 58; Li *et al*., 1998*c*: 232–233); Robert Island (Bonner & Lewis Smith, 1985: 88); Livingston Island (Lindsay, 1971: 76 as *Barbilophozia* sp.; Ochyra & Váňa, 1989*b*: 217; Sancho *et al*., 1999: 321); Deception Island (Lewis Smith 1984*b*: 56; 1984*c*: 29; Ochyra & Váňa, 1989*b*: 217). WEST ANTARCTIC PENINSULA: Davis Coast (Stephani 1911: 22–23 as *Lophozia floerkei*; Skottsberg, 1912: 8 as *L. floerkei*); Danco Coast (Stephani 1901: 4; 1905: 8; 1906: 152; all as *Lophozia floerkei*; Müller, 1910: 636; Skottsberg 1912: 9 as *L. floerkei*; Grolle 1960*a*: 564; Steere 1961: 30; Corte 1962: 7 as *Orthocaulis floerkei*; Lewis Smith & Corner, 1973: tab. V; Bonner & Lewis Smith, 1985: 106; Ochyra & Váňa 1989*b*: 216–217; Leeuw *et al.*, 1998: 473, 477 as *Barbilophozia* sp.); Graham Coast (Stephani, 1911: 22–23 as *Lophozia floerkei*; Schuster 1969*b*: 347; Fenton & Lewis Smith, 1982: 219; Lewis Smith & Corner, 1973: tab. V; Bonner & Lewis Smith, 1985: 54; Ochyra and Váňa 1989*b*: 216).

2. CRYPTOCHILA R. M. SCHUST.

Cryptochila R. M. Schust., J. Hattori Bot. Lab. **26**: 284. 1963. – HOLOTYPE: *Cryptochila pseudocclusa* (Hodgson) R. M. Schust. (*Jamesoniella pseudocclusa* Hodgson).

Plants small to medium–sized, 1–10 cm long, 1.0–2.5 mm wide, in loose deep tufts, somewhat lustrous, greenish to blackish- or reddish-green. *Stems* mostly ascending or erect, rigid, light brown to red- or blackish-brown, simple or rarely ventral-intercalary branched, frequently with microphyllous, prostrate stolons, in transverse section with 3–6-stratose cortex of small, thick-walled cells sharply set off from larger, firm-walled medullary cells or cortical and medullary cells weakly or undifferentiated. *Rhizoids* rare, only on stolons on larger plants or scattered on the ventral side of smaller plants. *Leaves* succubously to nearly transversely inserted, unlobed, distinctly short- to long-decurrent, entire-margined; leaf cells mostly thick-walled, with small trigones, arranged in regular concentric rows, becoming short-rectangular in the middle of the basal part; cuticle smooth. *Underleaves* highly reduced, filiform composed of 1–4 cells. *Dioecious*. *Androecia* intercalary; male bracts saccate, smaller than the leaves, with a single antheridium on biseriate stalk; paraphyses usually present in bract axils, hairy, needle- or scale-like. *Gynoecia* terminal, with involucral innovations below; female bracts larger that the leaves, lobate-laciniate; bracteoles mostly united at least with one bract. *Perianth* fusiform, strongly plicate with 5–10 plicae, often twisted, contracted to the mouth. *Capsule* wall 5–7-stratose; outer wall much thicker than the others, with strong, nodulose thickenings; inner walls thinner, with semiannulate thickenings. *Spores* globose, brown, verrucose, 13–17 in diameter; elaters bispiral; spore/elater width ratio about 2 : 1.

A small austral genus consisting of six species widely distributed in the temperate areas in the *Nothofagus* zone in the Southern Hemisphere, with only one species penetrating deeply into the tropics at high elevations. Grolle (1971*b*) monographed this genus and divided it into two subgenera, monotypic subgen. *Nigritula* Grolle restricted to New Zealand and the type subgenus consisting of the remaining five species, one of which extends to the Antarctic.

1. *Cryptochila grandiflora* (LINDENB. & GOTTSCHE) GROLLE FIG. 48

Cryptochila grandiflora (Lindenb. & Gottsche) Grolle, Feddes Repert. **82**(1): 19. 1971. – *Jungermannia grandiflora* Lindenb. & Gottsche *in* Gottsche, Lindenb. & Nees, Syn. Hep. **5**: 673. 1847. – *Jamesoniella grandiflora* (Lindenb. & Gottsche) J. B. Jack & Steph., Hedwigia **31**: 13. 1892. – TYPE: Habitat prope Valdiviam in regno Chile, unde attulit cl. Gay (Mont. in Hb. L. et G.) [HOLOTYPE: W-LINDENBERG!; ISOTYPE: PC-MONT!, S!].

Cryptochila grandiflora (Lindenb. & Gottsche) Grolle fo. *tenuiretis* Grolle, Br. Antarct. Surv. Bull. **28**: 84. 1972, *nom. nud.* – ORIGINAL MATERIAL: All material from South Sandwich Islands including Leskov Island, Candlemas Island and Bellingshausen Island collected by Longton and Holdgate (see “Specimens examined” section) was included in this form – AAS!, KRAM!, ***syn. nov.***

Plants medium-sized to relatively large, (1–)2–5(–8) cm long, in loose tufts, somewhat glistening, yellowish-green, greenish- to blackish-brown or reddish- to yellowish-brown, sometimes blackish. *Stems* ascending from the basal system of stolons, sometimes with intercalary microphyllous stolons, straight, rigid, reddish- or blackish-brown, in transverse section 15–20 cells high, with 3–4-stratose cortex of small, 15–20 µm wide, cells with strongly incrassate walls, sharply demarcated from the larger, collenchymatous, thin-walled internal cells. *Leaves* slightly succubous to nearly subtransverse, suborbicular to subovate, convex, long-decurrent on both sides, usually longer on the dorsal than on the ventral side; leaf cells with evenly thickened walls, without trigones, marginal cells 12–16 × 12–20 µm, median 15–25 µm, at the base forming a short vitta of short-rectangular cells, 15–20 × 45–70 µm; cuticle smoth. *Underleaves* highly reduced, filiform, composed of (1–)3–4 cells in 1 row. *Dioecious*. *Female inflorescence* terminal with involucral innovations below; female bracts larger than the leaves, obovate, mostly ciliate to lobate-ciliate; bracteoles united with one bract. *Perianth* fusiform, deeply 5–6-plicate, twisted above, entire to crenulate at the mouth. *Spores* globose, 16–17 µm in diameter; elaters bispiral.

Taxonomic and nomenclatural notes. — The species was originally described as *Jungermannia grandiflora* by Gottsche *et al.* (1847) from material collected in the Valdivian province of Chile, and subsequently transferred to *Jamesoniella* by Jack and Stephani (1892) where it was residual until Grolle (1971*b*) moved it to *Cryptochila*.

Cryptochila grandiflora is very variable in the size, habit and colour and, accordingly, various phenotypes were given taxonomic recognition. Grolle (1971*b*) recognised seven heterotypic synonyms for taxa described from various parts of its wide geographical range. In addition, subapical leaf cells are subject to considerable variation which is correlated with the size of the plants. Grolle (1972*a*) intended to recognise the plants from the South Sandwich Islands as fo. *tenuiretis* but this name has never been validly published. As a typical *nomen nudum* it is here reduced to synonymy with *C. grandiflora*. The Antarctic plants are generally smaller, apparently because of the harsh climatic conditions, and their leaf areolation is smaller than that in the luxuriant plants from lower latitudes, although large plants of this species are also frequently found in more favourable habitats.

Differentiation. — *Cryptochila grandiflora* may be recognised by its undivided, suborbicular, long-decurrent leaves, the almost total lack of the underleaves and the cell texture.

Reproduction in Antarctica. — Mostly sterile, but sporophytes are occasionally produced.

Habitat. — On volcanic ash and debris, on rock ledges and on gravel, usually in sheltered and moist situations.

World range. — A south-pan-temperate species widespread in the *Nothofagus* zone in southern South America, ranging from Central Chile and the Juan Fernandez Islands to Tierra del Fuego and the Falkland Islands (Fig. 49). Additionally, it has been recorded from all sub-Antarctic islands, southern Africa, south-eastern Australia, Tasmania and New Zealand. As with many austral cool-adapted bryophytes *Cryptochila grandiflora* penetrates deeply into the tropics and so far it has been recorded from south-eastern Brazil, the Andes of Peru and Colombia, Guatemala, Réunion and New Guinea and Borneo (Grolle, 1971*b*) (Fig. 49, inset).

Distribution in Antarctica. — It occurs principally on the South Sandwich Islands where it is widespread and locally common and abundant on some islands. It is also known on another volcanic island, namely Deception Island in the South Shetland Islands (Fig. 50).

Specimens examined. — SOUTH SANDWICH ISLANDS. **LESKOV ISLAND.** Summit ridge, *ca* 100 m, *Convey 245C & 246B* (AAS, KRAM) and *ca* 200 m, *Longton 502B & 506* (AAS, KRAM); summit ridge, near centre of crest, *ca* 225 m, *Holdgate 834B* (AAS, KRAM); east side of summit ridge, *Convey 249C, 250A & 251D* (AAS, KRAM); north end of island, *Longton 517* (AAS, KRAM). **CANDLEMAS ISLAND.** Lucifer Hill, base of cinder cone south of south-west crater, *Convey 108B* (AAS, KRAM); Lucifer Hill, north crater, *Convey 119A* (AAS, KRAM); Lucifer Hill, south-west crater, *Convey 176B, 177, 178A & 213B* (AAS, KRAM); Lucifer Hill, south-east slope, *Convey 214A* (AAS, KRAM); Lucifer Hill, north-west ridge active fissure, *Convey 217A, 219C, 220C, 223C, 224C, 225B, 228A & 241A* (AAS, KRAM); Lucifer Hill, summit of west supporting ridge of gully above Clinker Gulch, *Convey 234B & 235B* (AAS, KRAM); Lucifer Hill, south edge of shallow gully above Clinker Gulch, *Convey 124B, 125B, 126B, 127B, 129D, 135B, 142C, 144B, 149B, 150, 151C, 154B & 155A* (AAS, KRAM); Clinker Gulch, *Convey 156D, 162C, 163B,*

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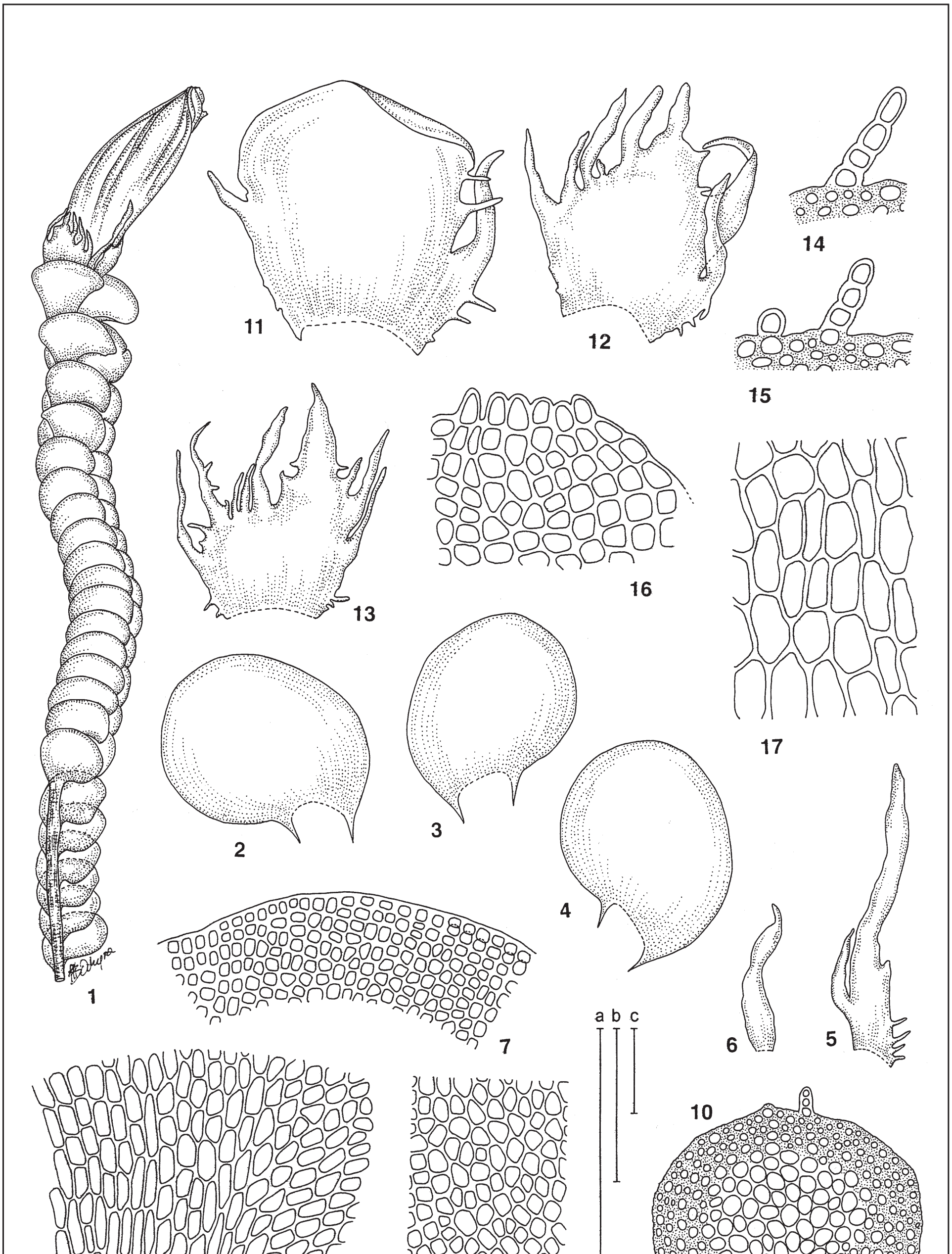
FIGURE 48. *Cryptochila grandiflora*. **1**. Portion of perianth-bearing shoot, lateral view. **2–4**. Leaves. **5–6**. Outline of paraphyses. **7**. Laminal cells at leaf apex. **8**. Mid-leaf cells. **9**. Basal cells in middle part of leaf. **10**. Transverse section of mature stem. **11–13**. Involucral bracts. **14–15**. Paraphyllia. **16**. Sector of perianth mouth. **17**. Cells in median part of perianth. (All from *Convey 177*, KRAM.) Scale bars: a – 5 mm (1); b – 1 mm (2–6, 11–13) and 100 µm (14–17); c – 100 µm (7–10).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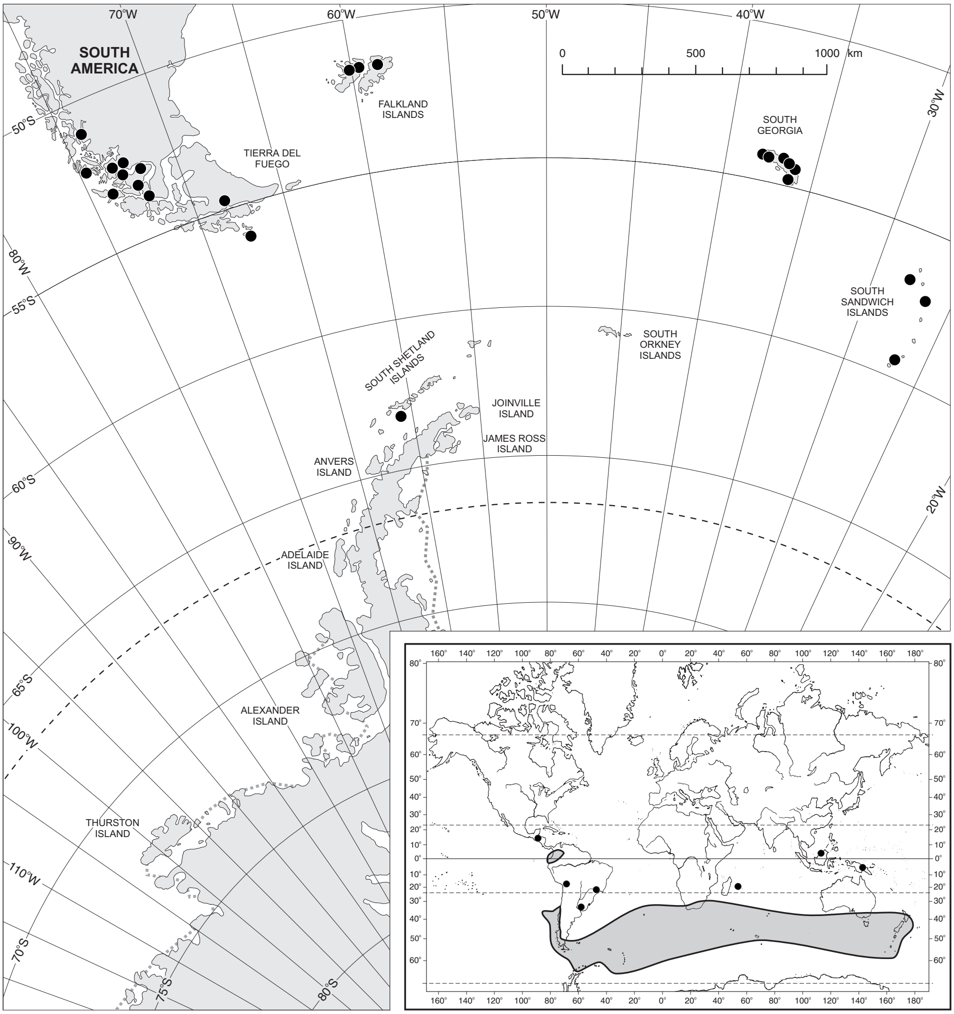

FIGURE 49. Distribution of *Cryptochila grandiflora* in the Antarctic and Fuegian region. Inset: global distribution.

164B, 166C, 179B, 182B, 185B & 237A (AAS, KRAM); west end of Breakbones Plateau, *Convey 197A, 198, 201B, 202A & 203B* (AAS, KRAM); Breakbones Plateau, *Convey 208A, 209A, 211 & 212B* (AAS, KRAM); between lagoons and most southerly exposed lava ridge, 65–100 m, *Longton 574, 575 & 576* (AAS, KRAM); north od western lagoon, *ca* 50 m, *Longton 693A, 694, 695 & 711* (AAS, KRAM); north of eastern lagoon, *ca* 50 m, *Longton 783A* (AAS, KRAM); between western lagoon and active cone, *ca* 35 m, *Holdgate 441 & 442B* (AAS, KRAM). **BELLINGSHAUSEN ISLAND**. South slope of cone (fumarole 2), *ca* 75 m, *Holdgate 811D, 812D, 819, 820C, 827B, 828B, 830B, 839C, 840A & 441A* (AAS, KRAM) and *Convey 29C & 49C* (AAS, KRAM); S slopes of main of main cone (fumarole 1),

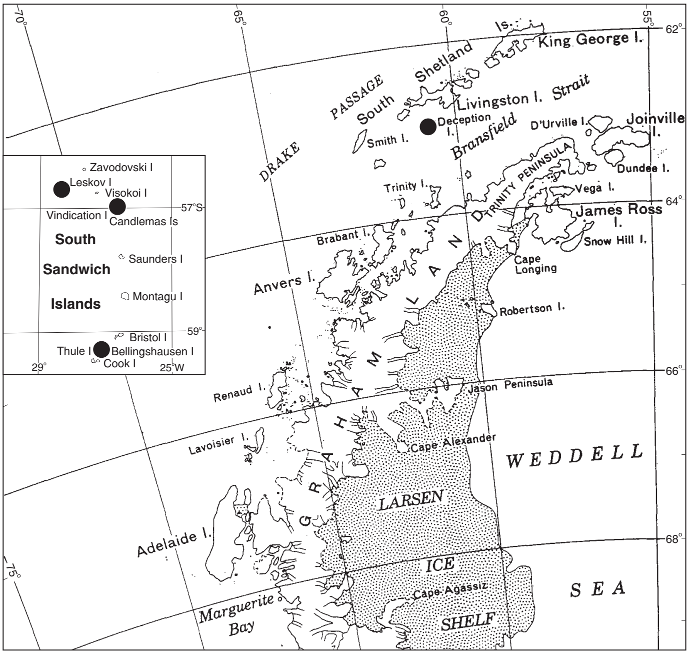

FIGURE 50. Distribution of *Cryptochila grandiflora* in the Antarctic.

ca 100 m, *Holdgate 405B, 409A, 410A, 413, 414 & 416B* (AAS, KRAM) and *Convey 25C & 51B* (AAS, KRAM); crater rim west of access point, *ca* 170 m, *Convey 30A, 31, 32B, 35, 39A, 41A, 42A & 46A* (AAS, KRAM); immediately to west of southern access to crater lip, 150 m, *Convey 53A, 54A, 56D & 57A* (AAS, KRAM); within crater, at south-east rim, *Holdgate 824B* (AAS, KRAM); east end of crater rim, *Holdgate 814C* (AAS, KRAM).

SOUTH SHETLAND ISLANDS. **DECEPTION ISLAND**. North side of Vapour Col, 400 m, *Mason 36A* (AAS, KRAM, PRC).

Literature records. — SOUTH SANDWICH ISLANDS: without indication of the island (Lewis Smith, 1993: 322); Leskov Island (Gimingham & Lewis Smith, 1970: 767 as *Jamesoniella grandiflora*; Grolle, 1971*b*: 21; 1972*a*: 84; Longton & Holdgate, 1979: 10; Lewis Smith, 1979*b*: 60; Bonner & Lewis Smith, 1985: 60; Ochyra & Váňa, 1989*b*: 217; Convey *et al.*, in press); Candlemas and Bellingshausen Islands (Gimingham & Lewis Smith, 1970: 767–768 as *Jamesoniella grandiflora*; Grolle, 1971*b*: 21; 1972*a*: 84; Longton & Holdgate, 1979: 10; Lewis Smith, 1979*b*; 60; Bonner & Lewis Smith, 1985: 290; Ochyra & Váňa, 1989*b*: 217; Convey *et al.*, in press).

3. LOPHOZIA (DUMORT.) DUMORT.

Lophozia (Dumort.) Dumort., Recueil Observ. Jung.: 17. 1835. – *Jungermannia* L. sect. *Lophozia* Dumort., Sylloge Jung. Eur. Indig.: 53. 1831. – LECTOTYPE: *Lophozia ventricosa* (Dicks.) Dumort. (*Jungermannia ventricosa* Dicks.) (*fide* Kitagawa, 1965: 271).

Plants small to medium-sized, green, yellowish, brownish, bluish or reddish. *Stems* creeping, prostrate to ascending, sometimes suberect, simple or sparingly lateral-intercalary (*Plagiochila*-

type) or terminally (*Frullania*-type) branched without stolons and flagellae, relatively slender, in transverse section 6–20 cells high, slightly dorsiventrally flattened, with cortical cells usually thin- to slightly thick-walled and medulla in ventral half of small, short and narrow cells, soon mycorrhizal and in part destroyed and brownish and in dorsal half of large, hyaline and pellucid cells. *Rhizoids* hyaline, pale brown or yellowish, scattered along the shoots. *Leaves* succubously to nearly transversely or nearly horizontally inserted, suborbicular to rectangular, usually widest at or near the middle, symmetrically or slightly asymmetrically bilobed, with postical lobe often somewhat wider than antical lobe, sometimes also 3–4-lobed; lobes triangular; margins plane or slightly recurved, entire on eroso-dentate on gemmiferous leaves; leaf cells variable, mostly thin-walled with trigones, but also thick-walled and nearly without trigones. *Underleaves* absent or rare, small, oval or lanceolate or bilobed. *Gemmae* on the leaf lobes or margins, mostly 2-celled, stellate or irregularly angular, sometimes nearly smooth, oval, ovate, subquadrate or spherical in outline. *Dioecious* or *paroecious*, rarely *autoecious*. *Androecia* on main shoots, becoming intercalary; male bracts saccate, 2(–3)-lobed, with 1–4 antheridia on 1–2-seriate stalk; paraphyses occasional, subulate or oval. *Gynoecia* terminal; female bracts larger than the leaves, 2–4-lobed; bracteoles mostly present, free or connate at least with one bract. *Perianth* cylindrical to oblong-cylindrical, plicate at least above, gradually tapering to the mouth; perigynium absent. *Capsule* ovoid, with (2–)3–4(–5)-stratose wall; epidermal cells somewhat thicker than those of inner layers, with nodular thickenings; inner cells with semiannular thickenings. *Spores* 10–18 μm in diameter; spore/elater width ratio mostly 2 : 1.

Lophozia is a large and very difficult genus to circumscribe. It is mostly recognised by considering a suite of features including bilobed or predominantly bilobed and obliquely to almost transverse antically leaves, lacking or with very few underleaves, mostly stellate or angular gemmae, terminal or lateral intercalary branching, dorsiventrally differentiated stem medulla and free, terete and distally plicate perianth. The genus consists of about 80 species (Váňa, 1999) and is usually subdivided into a number of subgenera some of which, including *Barbilophozia* and *Leiocolea* and sometimes also *Isopaches* and *Protolophozia* with *Schistochilopsis*, are considered by some authors as genera in their own right. The majority of species is distributed in cool and temperate regions of both Hemispheres, with only a small fraction of taxa is known from high elevations in tropical mountains. The genus is in need of modern taxonomic revision but until now only subg. *Protolophozia*, having a predominantly austral distribution, has been monographed on a worldwide basis (Schuster & Engel, 1975).

Two species belonging to the type subgenus have been recorded in Antarctica, although the identity of *Lophozia* cf. *groenlandica* cannot be definitely ascertained because of the incompleteness of the material, especially its sterility and the lack of oil-bodies. The two species can be differentiated in the following couplet.

KEY TO THE ANTARCTIC SPECIES OF *LOPHOZIA*

1. Gemmae mostly rare or nearly absent, only occasionally copious, purple to vinaceous; underleaves absent . . . . **1. *L. excisa***
1. Gemmae copious, yellowish-green or occasionally fuscous on entirely brown plants; underleaves sometimes present . . . . **2. *L.* cf. *groenlandica***

1. *Lophozia excisa* (DICKS.) DUMORT. FIGS 51–52

Lophozia excisa (Dicks.) Dumort, Recueil Observ. Jung.: 17. 1835. – *Jungermannia excisa* Dicks., Pl. Crypt. Brit. Fasc. **3**: 11, *t. 8, f. 7a*. 1793. – TYPE: [Britaniae] in sylvosis umbrosis humidis.

Lophozia propagulifera (Gottsche) Steph., Sp. Hepat. **2**: 139. 1901. – *Jungermannia propagulifera* Gottsche *in* Neumayer, Deutsch. Exp. Int. Polarforsch. **2**: 451. 1890. – TYPE: Dr Will Nr. 35; im obersteb Rasen. Süd-Georgien, Bachgrund oberhalb der Pinguinbay, 26. Januar 1883 [LECTOTYPE (*fide* Grolle, 1972*a*: 89): "№ 35 varia. Jungermannia propagulifera G. Original Gottsche Rasen 1. Bachgrund oberhalb der Pinguinbay. Süd-Georgien. 26/I.83 W.[ill]" – M!]. First reduced to synonymy by Schuster (1969*b*: 512, 521).

Lophozia propagulifera (Gottsche) Steph. fo. *densa* Grolle, Br. Antarct. Surv. Bull. **28**: 84. 1972, *nom. nud.* – ORIGINAL MATERIAL: South Sandwich Islands, Visokoi Island, Finger Point, *Longton 753* – AAS!, KRAM!, ***syn. nov.***

Plants variable in size and appearance, mostly to 1.5 cm long with leafy shoots 0.5–2.0 mm wide in dense or open mats, tufts or patches, soft-textured or flaccid, mostly pale to dark green or yellow-green or often tinged, especially above, with red, vinaceous-red, purplish-red, purple, brown or reddish-brown. *Stems* prostrate to creeping or erect in tufts of mosses, simple or sporadically lateral-intercalary branched, in transverse section 15–20 cells high, with weakly differentiated cortex of thin-walled, barely smaller cells or subequal to the dorsal medullary cells and with cells in ventral part of medulla smaller, strongly mycorrhizal and brownish with age. *Rhizoids* numerous, long, hyaline, dispersed on the ventral surface throughout the stem. *Leaves* succubously oriented, spreading, distant to contiguous, ovate to broadly quadrate, slightly wider than long when well developed, mostly slightly unequally bilobed, rarely trilobed, to 0.3–0.5 of their length, entire-margined; lobes broadly triangular, apiculate to acute; leaf cells thin-walled, with small to nearly absent trigones, marginal 22–30 µm, median 25–30 × 30–35(–40) µm; cuticle smooth. *Underleaves* absent. *Gemmae* infrequent at the apices of leaf lobes, mostly vinaceous, 1–2-celled, polygonal, 22–30 × 28–35 µm. *Paroecious*, highly proterandrous species. *Male bracts* similar to the leaves and only slightly saccate, mostly with one tooth at the base and 1–2(–3) antheridia on uniseriate stalk. *Female bracts* larger than the leaves, slightly crispate, mostly edentate; bracteoles oblong to lanceolate, united with one bract. *Perianth* cylindrical-clavate, plicate distally, contracted to the mouth. *Capsule* ovoid, reddish-brown; capsule wall 3–4-stratose; epidermal layer with nodular thickenings; inner layers with incomplete to almost complete semiannular bands. *Spores* verrucose, brown, 14–17 µm in diameter; elaters bispiral, 7.5–8.5 µm thick; spore/elater width ratio 2 : 1.

Taxonomic and nomenclatural notes. — *Lophozia excisa* is one of the earliest known liverwort species. It was described by Dickson (1793) from British material but, unfortunately, no specimens suitable for typification of this early name are available in the Dickson herbarium at BM. Therefore the interpretation of this taxon is based on the traditional opinion of various workers, which must inevitably lead to serious taxonomic and nomenclatural problems. A similar problem occurred with *Lophozia ventricosa*, another species recognised by Dickson (1790), which also cannot be typified because there is no suitable material remaining in the Dickson herbarium, and this species was selected as lectotype of the generic name *Lophozia* (Kitagawa, 1965). However, Grolle and Long (2000) selected a neotype for this species name and this is a logical solution because, even if the type is present, its oil-body character could not be ascertained.

Stephani (1901, 1905) reported from some stations in the western Antarctic Peninsula region *Lophozia propagulifera*, a species originally described from

South Georgia by Gottsche (1890) as *Jungermannia propagulifera*. Schuster (1969*b*) reduced this name to synonymy with *L. excisa*, though he did not examine original material; Grolle (1972*a*) still accepted the specific distinctness of *L. propagulifera*. Having examined the original material of this species, as well as the specimens studied by Stephani (1901, 1905), we concur with Schuster's (1969*b*) decision. We could not find any discernible difference between these and other plants currently interpreted as *L. excisa*, and phenotypes similar to or identical with the South Georgian type of this species occur commonly throughout the maritime Antarctic.

Grolle (1972*a*) recognised one plant from the South Sandwich Islands as *Lophozia excisa* fo. *densa* but he did not provided a Latin description, thus invalidly publishing this name. We reduce it to synonymy with *L. excisa* since, except for the very small size of the plant, we could not find other characters which could warrant recognition of it as separate taxon, and certainly this is merely an enviromentally-induced variant of the species.

Differentiation. — Although *Lophozia excisa* is an extremely polymorphous species, it can usually be easily recognised in the Antarctic. Fertile plants are distinct by the paroecious inflorescence but, unfortunately, they are rarely present in this region. Sterile plants are best distinguished by the thin-walled cells with small trigones in the bilobed leaves and especially by the gemmae which, if present, are purple to vinaceous. The latter character is especially important for distinguishing this species from *L. groenlandica* which produces copiously yellowish-green or occasionally fuscous gemmae.

Reproduction in Antarctica. — Fertile plants are seldom found, but the species propagates effectively by gemmae, which are produced by most populations, often in abundance.

Habitat. — It occurs most often in sheltered habitats, usually intermixed with various mosses such as *Bartramia patens*, *Chorisodontium aciphyllum*, *Pohlia nutans*, *Polytrichastrum alpinum* and *Polytrichum strictum*, usually in moist situations, in shaded rock crevices and fissures, on rock ledges covered with humus or soil, on scree slopes as well as on volcanic debris. It is a characteristic constituent of various communities of the fruticose lichen and moss cushion subformation, but occasionally it thrives on mats of *Sanionia georgico-uncinata* in communities of the moss carpet subformation.

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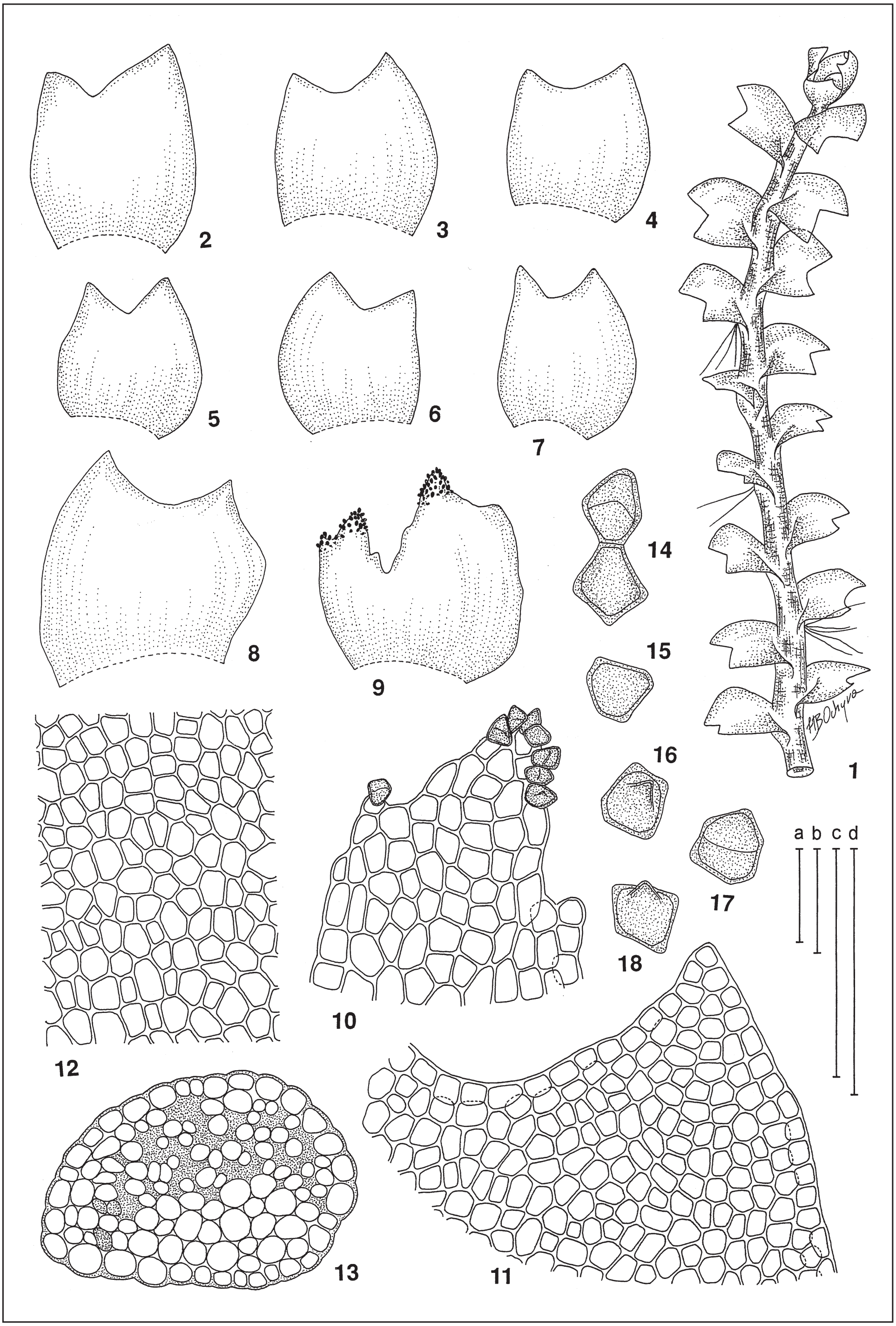
FIGURE 51. *Lophozia excisa*. **1**. Sterile shoot, dorsal view. **2–8**. Leaves. **9**. Gemmiferous leaf. **10**. Gemmiferous leaf lobe. **11**. Lobe apex. **12**. Mid-leaf cells. **13**. Transverse section of stem. **14–18**. Gemmae. (1–7, 11–13 from *Convey 155A*; 8 from *Lewis Smith 8998A*; 9–10, 14–18 from *Ochyra 346/80*; all in KRAM.) Scale bars: a – 100 μm (10–13); b – 1 mm (1); c – 1 mm (2–9); d – 100 μm (14–18).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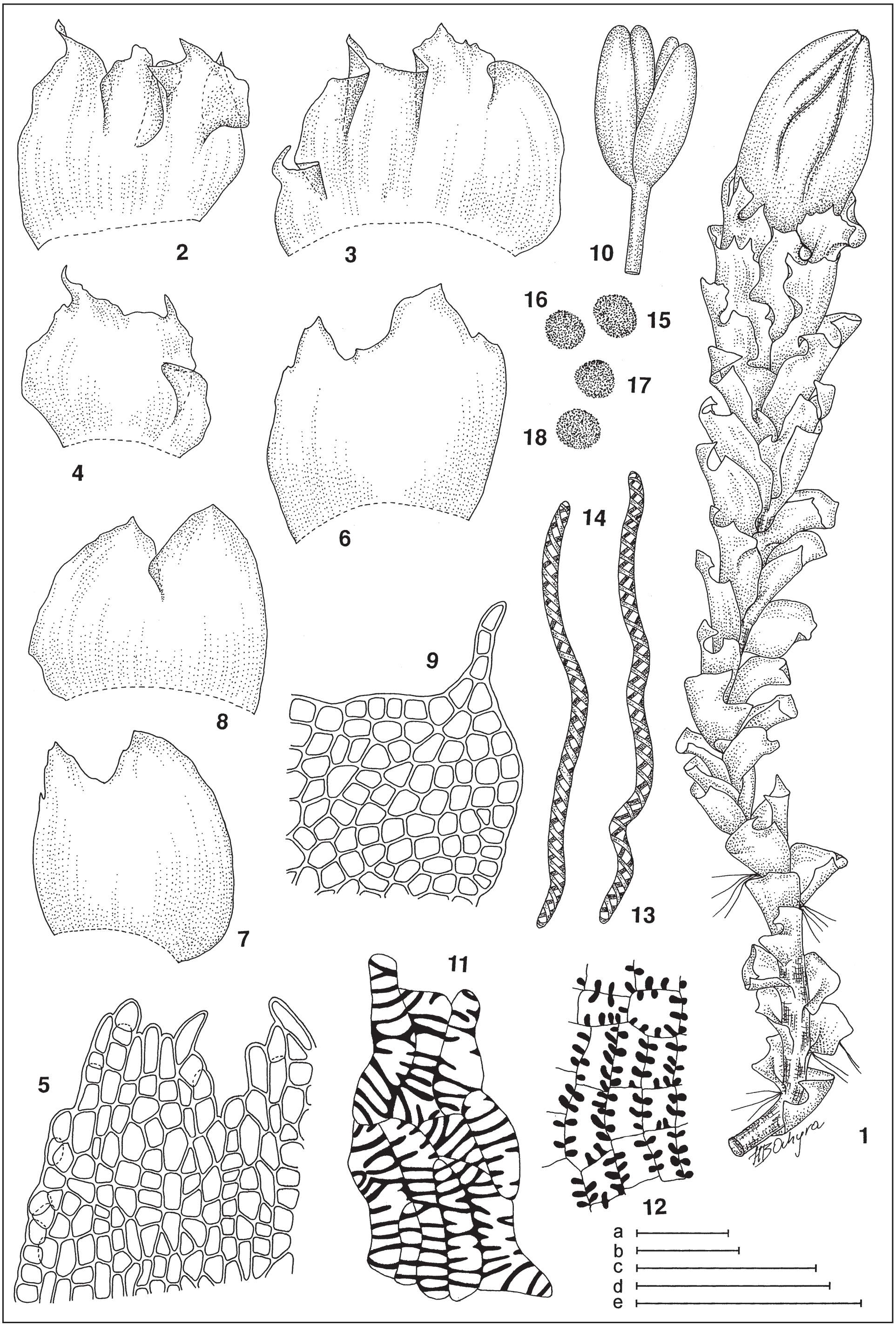
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World range. — A bipolar species having a wide, arctic-alpine distribution in the Holarctic and, in the Southern Hemisphere, known from the southernmost tip of South America, South Georgia and the Falkland Islands (Engel, 1990*a*) as well as from Antarctica and New Zealand (Schuster, 1969*c*; Szweykowski & Koźlicka, 1980*b*) (Fig. 53).

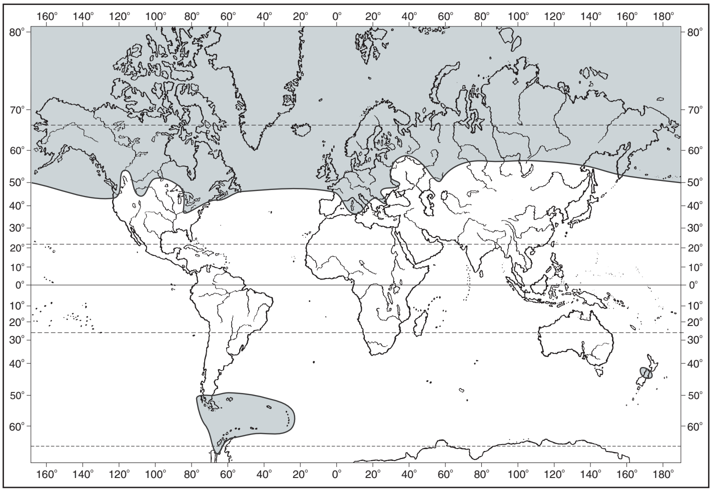

FIGURE 53. Global distribution of *Lophozia excisa*.

Distribution in Antarctica. — It is one of the most widespread and abundant of all Antarctic liverworts together with *Cephaloziella varians* and *Barbilophozia hatcheri*. It occurs throughout the maritime Antarctic from the South Sandwich Islands to northern Marguerite Bay, reaching its southernmost locality on Mushroom Island off the Fallières Coast at lat. 68°54'S (Fig. 54).

Specimens examined. — SOUTH SANDWICH ISLANDS. **LESKOV ISLAND**. North slopes of island, *ca* 100 m, *Holdgate 837B* (AAS, KRAM). **VISOKOI ISLAND**. Finger Point, *ca* 35 m, *Longton 753* (AAS, KRAM, M) *& 765* (AAS, KRAM). **CANDLEMAS ISLAND**. Lucifer Hill, east rim of south-west crater, *Convey 107G* (AAS, KRAM); Lucifer Hill, south-east lip of main crater, *Convey 117B* (AAS, KRAM); Lucifer Hill, south edge of shallow gully above Clinker Gulch, *Convey 127E, 138B, 151F & 155B* (AAS, KRAM); Clinker Gulch, *Convey 156E & 163D* (AAS, KRAM); Lucifer Hill, north-west ridge active fissure,

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FIGURE 52. *Lophozia excisa*. **1**. Shoot with mature perianth, dorsal view. **2–4**. Female bracts. **5**. Cells of perianth mouth. **6–8**. Male bracts. **9**. Lobe cells of female bract. **10**. Sporophyte. **11**. Epidermal cells of capsule wall. **12**. Inner cells of capsule wall. **13–14**. Elaters. **15–18**. Spores. (All from *Lewis Smith 8998A*, AAS.) Scale bars: a – 100 µm (5, 9); b – 1 mm (1); c – 100 µm (11–12); d – 1 mm (10); e – 1 mm (2–4, 6–8) and 100 µm (13–18).

Convey 238C & 240C (AAS, KRAM); between lagoons and most southerly exposed lava ridge, *Longton 571* (AAS, KRAM); north of western lagoon, *Longton 709B* (AAS, KRAM). **Bellingshausen Island**. Southern slopes of cone, 75 m, *Holdgate 839A* (AAS, KRAM).

SOUTH ORKNEY ISLANDS. **Coronation Island**. Olivine Point, *ca* 35 m, *Lewis Smith 147B* (AAS, KRAM); Saunders Point, *ca* 35 m, *Lewis Smith 18AA* (AAS, KRAM). **Lynch Island**. Without specific locality, 10 m, *Lindsay 988A* (AAS, KRAM) and 10–35 m, *Lewis Smith 529A* (AAS, KRAM); north-facing slope, 10 m, *Lindsay 988A* (AAS, KRAM). **Coffer Island**. Alt. 12–15 m, *Cameron & Kennett 11* (AAS, KRAM). **Powell Island**. Promontory on south-east coast, *ca* 135 m, *Lewis Smith 205C* (AAS, KRAM); north-west coast, 300 m, *Lewis Smith 241B* (AAS); promontory on west side of Falkland Harbour, *ca* 35 m, *Lewis Smith 279A* (AAS, KRAM). **Christoffersen Island**. Southern side, 50 m, *Richard 197B & 243C* (AAS, KRAM). **Laurie Island**. Scotia Bay, 50 m, Dec 1962, *Bellisio s.n.* (BA) and 85 m, Dec 1962, *Bellisio s.n.* (BA); Point Martin, 1000 m, Dec 1962, *Bellisio s.n.* (BA); Cabo Moneta, 200 m, Dec 1962, *Bellisio s.n.* (BA); Punta Diebel, 150 m, Dec 1962, *Bellisio s.n.* (BA). **Signy Island**. North-east of Express Cove, 50 m, *Lewis Smith 621* (AAS, KRAM); Knife Point, *ca* 35 m, *Lewis Smith 486B* (AAS, KRAM) and without elevation, *Lewis Smith 1848 & 1854* (AAS, KRAM); Factory Cove, slope behind the base, 35 m, *Lewis Smith 622A* (AAS, KRAM), 40 m, *Lewis Smith 306A* (AAS, KRAM), 75 m, *Lewis Smith 5201D & 5214* (AAS, KRAM) and 80 m, *Lewis Smith 5208* (AAS); Factory Cove, south of the base, 100 m, *Lewis Smith 470B* (AAS, KRAM); south-east shore of Factory Cove, 50 m, *Longton 1166* (AAS, KRAM); Factory Bluffs, *Lewis Smith 10891B* (AAS, KRAM); south of Berntsen Point, *ca* 35 m, *Lewis Smith 539A* (AAS, KRAM); north side of Observation Bluff, 15 m, *Lewis Smith 692A* (AAS, KRAM), 35 m, *Lewis Smith 540* (AAS, KRAM) and 65 m, *Lewis Smith 322* (AAS, KRAM); Paal Harbour, *ca* 80 m, *Lewis Smith 670B* (AAS, KRAM); Moraine Valley, west side of Rusty Bluff, 50 m, *Lewis Smith 551C* (AAS, KRAM), 80 m, *Lewis Smith 5227* (AAS, KRAM) and 100 m, *Lewis Smith 615* (AAS, KRAM); east side of Rusty Bluff, 100 m, *Lewis Smith 351C* (AAS, KRAM); hill 236 north of Gourlay Peninsula, 50 m, *Longton 1151* (AAS, KRAM); between Gourlay Peninsula and Lenton Point, *ca* 35 m, *Lewis Smith 476A* (AAS, KRAM). **Moe Island**. Spaull Point, 30–200 m, *Lewis Smith 5240B* (AAS, KRAM); without closer locality, 10–200 m, *Lewis Smith 5256* (AAS, KRAM).

SOUTH SHETLAND ISLANDS. **Elephant Island**. 2 km south-west of Endurance Glacier, 152 m, *Allison 28D* (AAS). **King George Island**. ***Admiralty Bay***: Demay Point, 50 m, *Ochyra 1389/80* (KRAM, PRC); Creeping Slopes, 60 m, *Ochyra 1235/80* (KRAM, PRC); Sphinx Hill, 100 m, *Ochyra 280/80* (KRAM, PRC); Rescuers Hills, 25 m, *Ochyra 4898/79* (AAS, KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 175], *4967/79 & 4969/79* (KRAM, PRC), 40 m, *Ochyra 289/80* (KRAM, PRC) and 45 m, *Ochyra 180/80* (KRAM, PRC); Ecology Glacier, 15 m, *Ochyra 706/80* (KRAM, PRC); Hala, 18 m, *Ochyra 5213/79* (KRAM, PRC) and 35 m, *Ochyra 5228/79* (KRAM, PRC); Upłaz, 50 m, *Ochyra 2359/80* (KRAM, PRC) and 60 m, *Ochyra 2354/80* (KRAM, PRC); Ubocz, 100 m, *Ochyra 2353/80* (KRAM, PRC) and 110 m, *Ochyra 2381/80* (KRAM, PRC); Jersak Hills, 100 m, *Ochyra 15069/79* (KRAM, PRC); Gdynia Point, 20 m, *Ochyra 1763/80* (KRAM, PRC); Mt. Belweder, 150 m, *Ochyra 1593/80* (KRAM, PRC); Klekowski Crag, 220 m, *Ochyra 2301/80* (KRAM, PRC); Ore Point, 3 m, *Ochyra 510/80* (AAS, KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 22]; Speil Point, 5 m, *Ochyra 556/80* (KRAM, PRC); Round Hill,

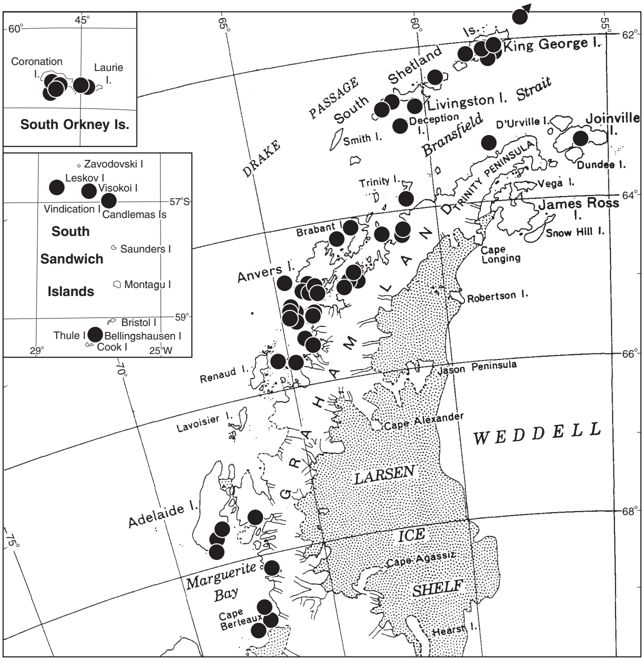

FIGURE 54. Distribution of *Lophozia excisa* in the Antarctic. The locality on Elephant Island is indicated by an arrow.

50 m, *Ochyra 534/80* (KRAM, PRC); Mt. Flagstaff, 120 m, *Ochyra 424/80 & 426/80* (KRAM, PRC); Moraine Point, 25 m, *Ochyra 491/80* (KRAM, PRC) and 30 m, *Ochyra 485/80* (KRAM, PRC); Stenhouse Bluff, 30 m, *Ochyra 2626/80, 2585/80 & 2596/80* (KRAM, PRC); Mt. Wawel, 40 m, *Ochyra 2126/80* (KRAM, PRC); Rembiszewski Nunataks, 150 m, *Ochyra 2732/80 & 2757/80* (KRAM, PRC). ***Fildes Peninsula***: Ardley Island, 10 m, *Ochyra 2497/80* (AAS, KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 124], *Komárková 547* (KRAM), 19 Dec 1988, *Li AN29* (AAS) and *Nikolaev s.n.* (LE, PRC); Bellingshausen Station, 15 m, *Ochyra 2409/80 & 2418/80* (KRAM, PRC); Bukhta Kamenistaya, *Nikolaev 35* (LE, PRC); without closer locality data, Dec 1988, *Macchiavello s.n.* (BA). ***Legru Bay***: Lions Rump, 150 m, *Lindsay 799B* (AAS, KRAM). ROBERT ISLAND. Coppermine Cove, 7 m, *Frödin N.3* (KRAM, NY, S). LIVINGSTON ISLAND. ***Byers Peninsula***: West Beach, between Smellie Point and Devils Point, 5 m, *Richard 28H & 29D* (AAS, KRAM); Laarger Point, 30 m, *Richard 28H & 29D* (AAS, KRAM); Ocoa Point, 20–75 m, *Richard 44D* (AAS, KRAM). ***Hurd Peninsula***: South Bay, 5 m, *Schulz 159* (Hb. Schulz, KRAM) and 35 m, *Schulz 130* (Hb. Schulz, KRAM). SNOW ISLAND. President Head, 5–10 m, *Richard 11A* (AAS, KRAM). DECEPTION ISLAND. South-west of Ronald Hill, *ca* 10 m, *Lewis Smith 62* (AAS, KRAM) and 8–15 m, *Longton 32B* (AAS); between Kroner Lake and Ronald Hill, *Longton 900* (AAS); Crater Lake, 15 m, *Lewis Smith 5648B* (AAS, KRAM).

WEST ANTARCTIC PENINSULA. TRINITY PENINSULA. Joinville Island, Mt. Alexander, 15–50 m, *Lewis Smith 3704* (AAS, KRAM) and 60 m, *Lewis Smith 3672A* (AAS, KRAM). DAVIS COAST. Astrolabe Island, 10–30 m, *Lewis Smith 4059* (AAS, KRAM); Trinity Island, 200 m, *Willey & G. Smith s.n. (Lewis Smith 700E)* (AAS, KRAM). DANCO COAST. Spring Point, *Komárková 464, 1191 & 1253* (KRAM); Cierva Point, *Komárková*

615A & 658 (KRAM); Centre Rocks, 7 Feb 1952, *Hässel de Menendez s.n.* (BA); Challenger Island, 2 Dec 1902, *Skottsberg 391* (S); Andrée Island, 30 m, *Lewis Smith 4041* (AAS, KRAM); Charlotte Bay, Recess Cove, 2–10 m, *Lewis Smith 3992 & 3993* (AAS, KRAM); Beneden Head, *Racovitza 233F* (G). ***Melchior Islands***: Omega Island, 2–10 m, *Lewis Smith 4126* (AAS). ***Brabant Island***: Claude Point, *Hankinson 118B* (AAS, KRAM). ***Anvers Island***: Cape Monaco, *Komárková 727* (KRAM); Hermit Island, *Lewis Smith 891B* (AAS, KRAM); Laggard Island, *ca* 15 m, *Longton 1296* (AAS, KRAM); Litchfield Island, Arthur Harbour, *Komárková 85A, 506 & 1107* (KRAM) and 10–25 m, *Lewis Smith 1968* (AAS, KRAM); Joubin Island, *Rastofer & Gnau PAL–21A* (US). **GRAHAM COAST**. Rasmussen Island, *Lewis Smith 1924A & 1925* (AAS, KRAM); Cape Tuxen, *ca* 15 m, *Corner 849* (AAS, KRAM) and *Lewis Smith 10672* (AAS), 200 m, *Corner 689* (AAS, KRAM) and 30–300 m, *Lewis Smith 4917* (AAS, KRAM). ***Petermann Island***: 50 m, *Scott 131B* (AAS, KRAM) and *Corner 722B* AAS, KRAM), 60 m, *Scott 123C* (AAS, KRAM) and 89 m, *Scott 134B* (AAS, KRAM). ***Argentine Islands***: Black Island, 10 m, *Corner 834* (AAS, KRAM); Uruguay Island, north-east side, 7 m, *Corner 595A & 597C* (AAS, KRAM); same island, *ca* 35 m, *Corner 818B* (AAS, KRAM); same island, *ca* 15 m, *Corner 438A* (AAS, KRAM); largest island between Irizar and Uruguay Island, *ca* 15 m, *Corner 343B* (AAS, KRAM); Galindez Island, *ca* 10 m, *Longton 1366* (AAS, KRAM), 15 m, *Longton 1256* (AAS, KRAM), 30 m, *Lewis Smith 3292* (AAS, KRAM) and *ca* 35 m, *Longton 1240 & 1241* (AAS, KRAM). ***Berthelot Islands***: north side of the largest island, *ca* 135 m, *Corner 622D* (AAS, KRAM). ***Grandidier Channel***: Darboux Island, 12–20 m, *Lewis Smith 3336* (AAS, KRAM); Leroux Bay, west side of Lahille Island, 2–5 m, *Lewis Smith 4329AB* (AAS, KRAM); Hook Island, *Schuster 68–510A* (US). **LOUBET COAST**. Blaiklock Island, 13–15 m, *Lewis Smith 851 & 852* (AAS, KRAM). ***Léonie Islands***: Lagoon Island, 10–25 m, *Lewis Smith 9183* (AAS, KRAM); north side of Léonie Island, 20 m, *Lewis Smith 8998A & 10649* (AAS, KRAM); Lagoon Island, 10 m, *Lewis Smith 3672B* (AAS, KRAM) and 35 m, *Lewis Smith 10647* (AAS, KRAM). **FALLIÈRES COAST**. Jenny Island, *Killingbeck 111B, 228A & 229B* (AAS, KRAM); north-east side of Neny Island, 50 m, *Lewis Smith 796* (AAS, KRAM); north side of Jenny Island, 15–50 m, *Lewis Smith 4721B* (AAS, KRAM); Terra Firma Islands, Alamode Island, *Poncet 3I* (AAS, KRAM); Mushroom Island, *Poncet 1DD* (AAS, KRAM) *& 1F* (AAS). ***Adelaide Island***: Rothera Point, 10 m, *Lewis Smith 8888* (AAS, KRAM), 25 m, *Fenton 48D* (AAS, KRAM) and 20–30 m, *Lewis Smith 1865* (AAS, KRAM); Stork Ridge, *Convey XIV/98* (AAS, KRAM).

Literature records. — SOUTH SANDWICH ISLANDS: Leskov, Visokoi, Candlemas and Bellingshausen Islands (Gimingham & Lewis Smith, 1970: 767; Grolle, 1972*a*: 84; Longton & Holdgate, 1979: 10 all as *Lophozia propagulifera*; Ochyra & Váňa, 1989*b*: 217. SOUTH ORKNEY ISLANDS: Powell Island (Bonner & Lewis Smith, 1985: 91 as *L. propagulifera*); Signy Island (Lewis Smith, 1985: 109; 1987: 240 as *L.* cf. *propagulifera*; Lewis Smith & Coupar, 1986: 194). SOUTH SHETLAND ISLANDS: Elephant Island (Allison & Lewis Smith, 1973: 187; Lewis Smith, 1979*a*: 235; both as *Lophozia* sp.; Ochyra & Váňa, 1989*b*: 217); King George Island (Ochyra *et al*., 1982: 261; Ochyra, 1984: 5, 18, 24; Ochyra *et al*., 1986: 55; Ochyra & Váňa, 1989*a*: 202; 1989*b*: 217; Myrcha *et al*., 1991: 163; Chen *et al*., 1993: 50; 1995: 137–139 both as *Marsupella boeckii*; Okada & Kanda, 1994: 58; Li *et al*., 1998*a*: 201 as *Marsupella boeckii*); Livingston Island (Schuster, 1969*b*: 516; Bonner & Lewis Smith, 1985: 155 as *L. propagulifera*; Sancho *et al*., 1999: 322);

Deception Island (Schuster, 1969*b*: 516; Lewis Smith, 1984*b*: 56; Lewis Smith, 1984*c*: 29, 32; Ochyra & Váňa, 1989*b*: 217). WEST ANTARCTIC PENINSULA. Danco Coast (Stephani, 1901: 4; 1902: 140; 1905: 8; Skottsberg 1912: 9; Steere, 1961: 30; Corte, 1962: 7; Bonner & Lewis Smith, 1985: 106 all as *L. propagulifera*; Ochyra & Váňa, 1989*b*: 217); Graham Coast (Schuster, 1969*b*: 516); Loubet Coast (Lewis Smith, 1995: 85 as *Barbilophozia hatcheri*; Lewis Smith & Convey, in press); Fallières Coast (Lewis Smith & Poncet, 1987: 34 as *Barbilophozia hatcheri*).

2. *Lophozia* cf. *groenlandica* (NEES) MACOUN FIG. 55

Lophozia cf. *groenlandica* (Nees) Macoun, Cat. Canad. Pl. **7**: 19. 1902. – *Jungermannia groenlandica* Nees *in* Gottsche, Lindenb. & Nees, Syn. Hepat.: 114. 1844. – *Sphenolobus groenlandicus* (Nees) Steph., Sp. Hepat. **2**: 164. 1902. – TYPE: Habitat in Groenlandia ad terram, denso caespite (Breutel et Curie in Hb. Flotoviano n. 2 [HOLOTYPE: STR (*non vidi*); ISOTYPE: W-LINDENBERG!].

? *Lophozia antarctica* R. M. Schust., Antarct. Journ. U.S. **4**(4): 103. 1969, *nom. nud.* – ORIGINAL MATERIAL: Antarctic Peninsula region, leg. R. M. Schuster, January/February 1969 (*non vidi*), ***syn. nov.***

Plants medium-sized, mostly in compact patches, 0.5–1.5 cm long with leafy shoots 0.8–1.8 mm wide, mostly yellowish-brown, rarely fuscous or bright yellowish-green. *Stems* prostrate to ascending, soft-textured, commonly terminal and lateral-intercalary branched with branches producing occasionally small-leaved but not microphyllous shoots, in transverse section with ventral cells much smaller, mycorrhizal, occupying 2/3 of the stem width. *Rhizoids* numerous, colourless to slightly fuscous, dispersed on the ventral surface of the stem. *Leaves* obliquely succubously oriented, contiguous to distant, lax, polymorphous, slightly concave, ovate to nearly circular, bi- or rarely also some leaves trilobed to 0.2–0.4 of the length, entire-margined; lobes mostly broadly triangular, acute to slightly obtuse; leaf cells thin-walled to feebly thick-walled, with small to rather distinct, never bulging trigones, marginal cells in the sinus mostly with brownish coloured walls, 18–25 µm wide at margins, 20–23 × 22–30 µm in mid-leaf; cuticle smooth; ventral merophytes relatively wide, mostly for 3–5 cells. *Underleaves* sometimes present, lanceolate to slightly bilobed. *Gemmae* frequent, produced at the apices of leaf lobes, yellowish-green, 1–2-celled, polygonal to quadrate, 14–20 µm. *Sterile* in Antarctica.

Taxonomic and nomenclatural notes. — Although recognised relatively early on the basis of plants collected from Greenland (Gottsche *et al.*, 1844), *Lophozia groenlandica* has been greatly misunderstood and usually considered to be conspecific with *L. wenzelii*. This confusion continues (Damsholt, 1994), but in the present treatment the concept of this species outlined by Schljakov (1975, 1980, 1998) is accepted because he has convincingly demonstrated the synonymy of *L. murmanica* Kaal., *L. heteromorpha* R. M. Schust. & Damsh. and *L. groenlandica*. On the other hand, *L. confertifolia* Schiffn. is here excluded from synonymy of *L. groenlandica* and this implies that this species must be also excluded from the hepatic flora of Central Europe. This interpretation of *L. groenlandica* has also been accepted in the latest checklist of European liverworts (Grolle & Long, 2000). However, plants considered by Schuster (1959, 1961, 1969*b*) as *L. groenlandica* are recognised by Schljakov (1975, 1980) to be a different species, *L. schusteriana* Schljak.

Differentiation. — The species is here named with some reservation because the Antarctic material is incomplete and some taxonomically critical characters, including the sexuality of the plants and oil-bodies, cannot be verified. In the vegetative characters the plants from Antarctica show perfect correspondence with the high Arctic plants of *Lophozia groenlandica* (including *L. murmanica* and *L. heteromorpha*). They are mostly yellowish-brown with a characteristically fuscous, not vinaceous, row of cells, at least in the sinus, the underleaves are very sporadically present and the trilobed leaves are not so common.

This species can be easily separated from *Lophozia excisa* by the very frequent, yellowish-green to fuscous, but never purple or vinaceous, gemmae which are mostly polygonal (not multiangulate). In addition, underleaves are occasional and wide ventral merophytes are also characteristic for *L. groenlandica*.

Although no material collected by Schuster (1969*a*) and provisionally named *Lophozia antarctica* has been available for examination, we believe that it may represent this species and therefore this *nomen nudum* is here provisionally considered as a synonym of *L. groenlandica*. R. M. Schuster (*in litt.*) stated that his plants produced abundant yellowish-green gemmae and may belong to *L. wenzelii*. However, this species should be excluded from consideration here since the material examined during the present research does not represent this taxon because of the different leaf insertion, leaf sinuses and the presence of underleaves.

Reproduction in Antarctica. — Fertile plants unknown; the species probably propagates here only by gemmae which are produced in abundance.

Habitat. — According to the scanty label data, this species occurs on sheltered vertical rocks, on ledges and in moist rock crevices and in sheltered hollows on peat banks dominated by *Chorisodontium aciphyllum* and *Polytrichum strictum*.

World range. — The geographical distribution of *Lophozia groenlandica* is imperfectly known owing to the taxonomic misinterpretation of this species. It seems to be essentially an arctic-alpine species, having a continuous range in the High Arctic, and occasionally found in mountains in the southern parts of the Holarcitc, for example in the Altai (Fig. 56). The present records are the first for this species in the Southern Hemisphere.

Distribution in Antarctica. — *Lophozia groenlandica* is here reported for the first time from the Antarctic and from the Southern Hemisphere. It appears to be very rare and widely scattered, known only from Signy Island in the South Orkney Islands, and from a few sites on the Danco and Graham Coasts on the west coast of the Antarctic Peninsula, extending to lat. 65°20'S on Green Island (Fig. 57).

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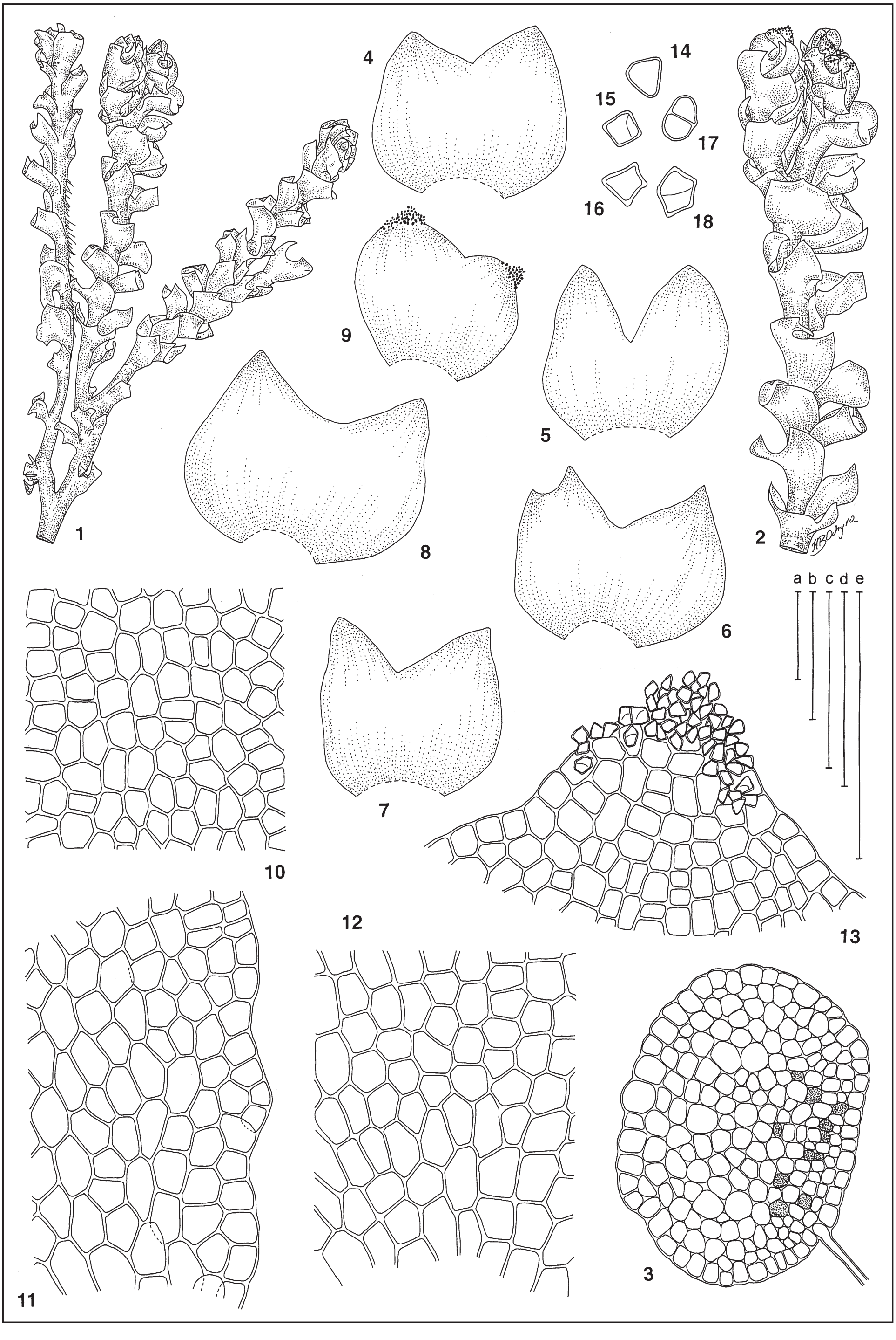
FIGURE 55. *Lophozia* cf. *groenlandica*. **1**. Sterile plant. **2–4**. Shoot in dorsal view. **3**. Transverse section of stem. **4–8**. Leaves. **9**. Gemmiferous leaf. **10**. Mid-leaf cells. **11**. Basal angular cells. **12**. Basal cells in the middle of insertion. **13**. Gemmiferous leaf lobe. **14–18**. Gemmae. (All from *Lewis Smith 3412*, AAS.) Scale bars: a – 100 μm (3) and 1 mm (2); b – 100 μm (10–13); c – 1 mm (4–9); d – 100 μm (14–18); e – 0.5 cm (1).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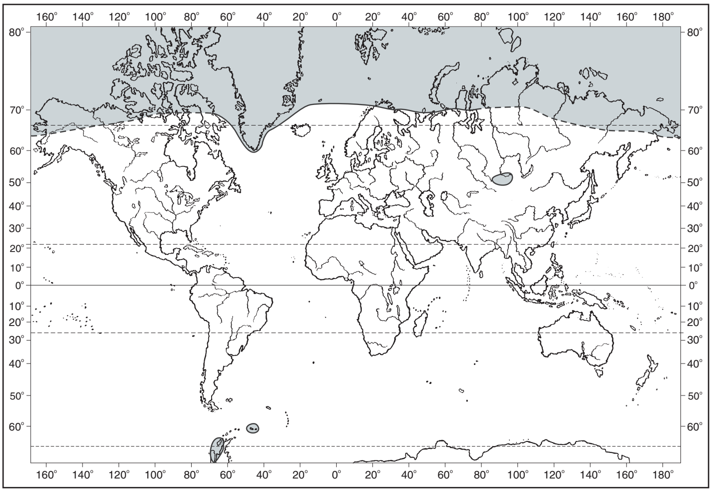


FIGURE 56. Global distribution of *Lophozia groenlandica*.

Specimens examined. — SOUTH ORKNEY ISLANDS. **SIGNY ISLAND**. Moraine Valley, 50 m, *Lewis Smith 411B* (AAS, KRAM) and without elevation, *Lewis Smith 1844* (AAS, KRAM); Observation Bluff, 40 m, *Lewis Smith 10857* (AAS, KRAM); Rusty Bluff, 50 m, *Lewis Smith 542* (AAS, KRAM); above Paal Harbour, *ca* 85 m, *Lewis Smith 681A* (AAS, KRAM).

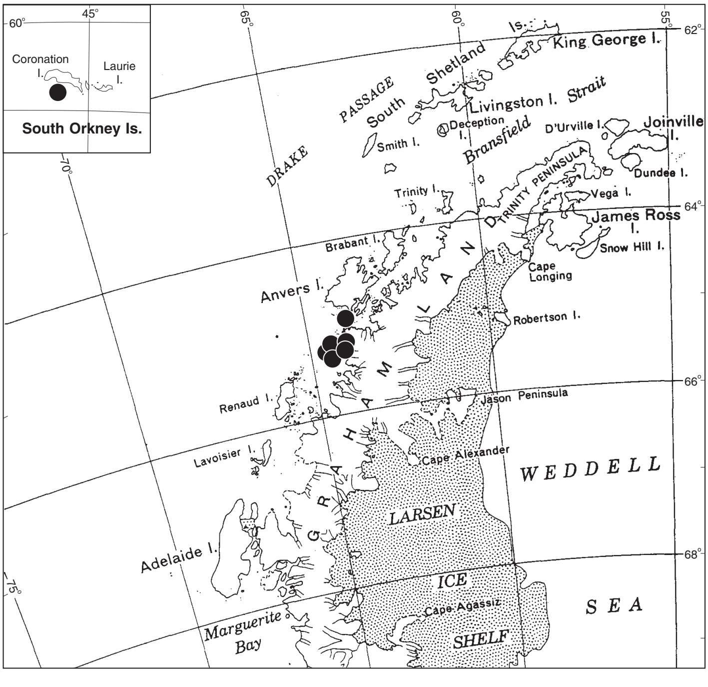


FIGURE 57. Distribution of *Lophozia* cf. *groenlandica* in the Antarctic.

WEST ANTARCTIC PENINSULA. **Danco Coast.** ***Anvers Island***: Laggard Island, *Longton 1295* (AAS, KRAM). **Graham coast.** Rasmussen Island, 100 m, *Corner 411B* (AAS, KRAM). Cape Tuxen, 15 m, *Lewis Smith 10672* (AAS, KRAM). ***Argentine Islands***: Galindez Island, Stella Creek, *ca* 15 m, *Longton 1328* (AAS, KRAM); same island, Meek Creek, *ca* 35 m, *Longton 1332* (AAS, KRAM); north end of Uruguay Island, 20 m, *Corner 739B* (AAS, KRAM). ***Berthelot Islands***: Green Island, 15–50 m, *Lewis Smith 3412* (AAS, KRAM).

Literature records. — West Antarctic Peninsula: without closer locality (Schuster, 1969*a*: 103 as *Lophozia antarctica*); Graham Coast (Bonner & Lewis Smith, 1985: 54 as *Barbilophozia hatcheri*).

4. ROIVAINENIA PERSS.

Roivainenia Perss. *in* Perss. & Grolle, Nova Hedwigia **3**: 43. 1955. – HOLOTYPE: *Roivainenia jacquinotii* (Mont.) Grolle (*Jungermannia jacquinotii* Mont.).

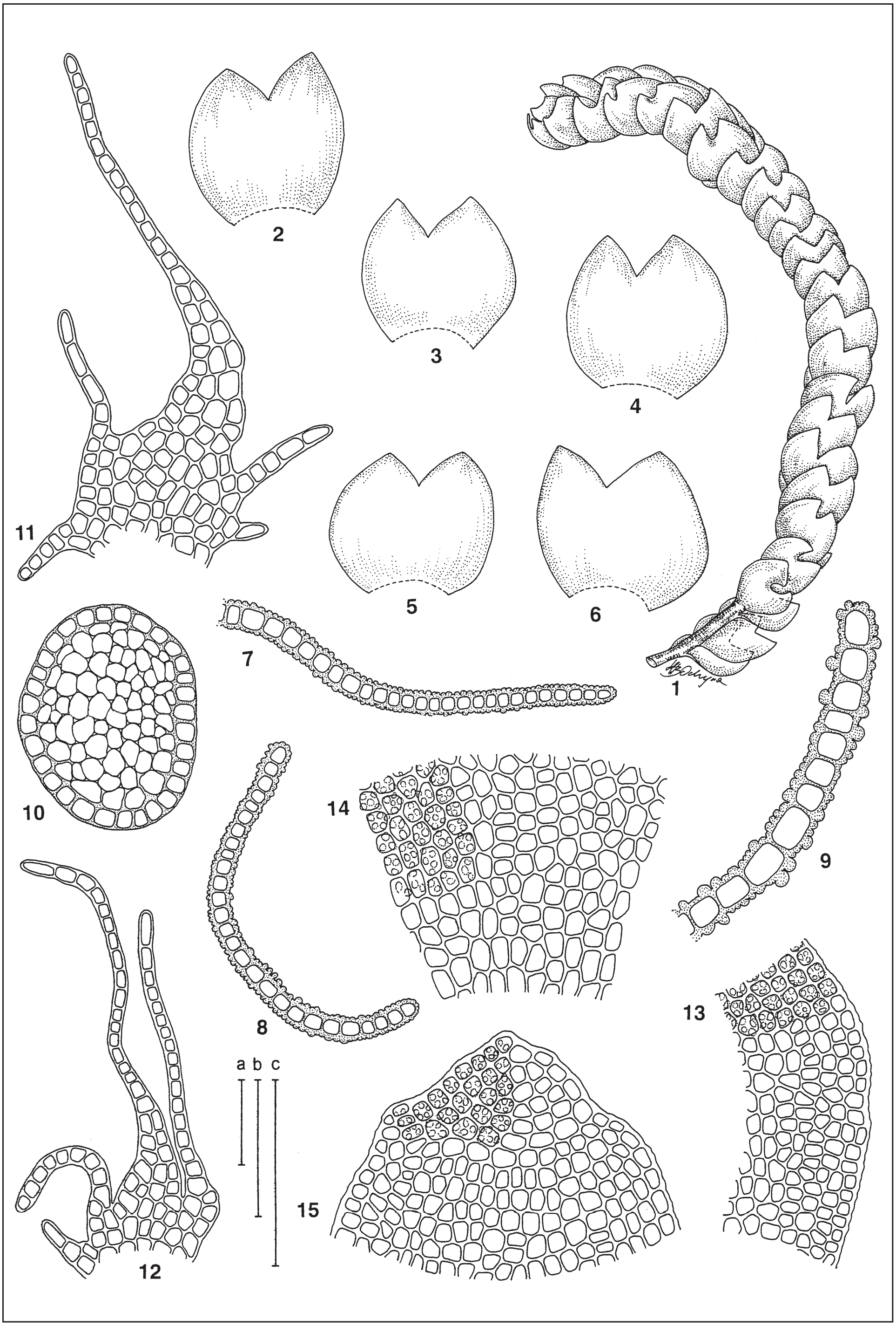
Plants medium-sized to relatively large and robust, in loose patches or dense tufts pale or yellowish-green, yellowish-brown to brown or reddish-brown. *Stems* prostrate, simple or occasionally terminally, lateral-intercalary or ventral-intercalary branched, rigid, brown, in transverse section with a unistratose cortex of thick-walled cells, surrounding a medulla of slightly larger cells with thin walls and minute trigones. *Rhizoids* pale, scattered on the ventral surface of the stem, arising at base of leaves and underleaves. *Leaves* contiguous to imbricate, succubously oriented, concave, in outline suborbicular to subcordate, bilobed to 0.3–0.5 of the length, sometimes with some laciniae at base; sinus acute, somewhat gibbous; lobes triangular, relatively wide, acute or long apiculate; leaf cells subquadrate, with thickened walls and minute or missing trigones; cuticle covered with large papillae. *Underleaves* absent or present. *Dioecious*. *Androecia* terminal, becoming intercalary; male bracts saccate, bearing a single antheridium with biseriate stalk. *Gynoecia* terminal; female bracts crispate, deeply laciniate. *Perianth* fusiform, 5–6-plicate at least distally, twisted or not at the mouth. *Capsule* ovoid, with 6–7-stratose wall; outer wall with nodular, inner with semiannular thickening. *Spores* reddish-brown, papillose; elaters bispiral; spore/elater width ratio 2 : 1.

A small antipodal monotypic genus consisting of a single species, *Roivainenia jacquinotii*, occurring in the *Nothofagus* zone in southern South America (Persson & Grolle, 1961). The Tasmanian *R. tasmanica* (Rodway) Grolle was another species given a name in this genus, but Grolle (1977) considered it to be conspecific with *Chandonathus squarrosus* (Hook.) Mitt. *ex* Schiff., thus leaving *Roivainenia* monotypic. *Roivainenia jacquinotii* has been collected only once in the Antarctic.

1. *Roivainenia jacquinotii* (MONT.) GROLLE FIG. 58

Roivainenia jacquinotii (Mont.) Grolle *in* Perss. & Grolle, Nova Hedwigia **3**: 44. 1961. – *Jungermannia jacquinotii* Mont., Ann. Sci. Nat. Bot. Sér. 2, **19**: 250. 1843. – *Chiloscyphus jacquinotii* (Mont.) Nees *in* Gottsche Lindenb. & Nees, Syn. Hepat. **2**: 185. 1845. – TYPE: In Freto Magellanico legerunt cl. d'Urville et cl. Jacquinot [HOLOTYPE: PC-MONT!].

Plants medium-sized to rather large, in loose patches or dense tufts pale or yellowish-green, yellowish-brown to brown or reddish-brown. *Stems* prostrate, 1–3 cm long, simple or occasionally terminally, lateral-intercalary or ventral-intercalary branched, rigid, brown, in transverse section 10–15 cells high, consisting of a single row of thick-walled cortical cells, 15–25 μm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wide, surrounding slightly larger medullary cells with thin walls and minute trigones. *Rhizoids* pale, scattered on the ventral surface of the stem, arising at base of leaves and underleaves. *Leaves* contiguous to imbricate, succubously oriented, concave, suborbicular to subcordate, bilobed to 0.3–0.5 of the length, entire-margined; sinus acute, somewhat gibbous; lobes triangular, relatively wide, acute or long apiculate. *Leaf cells* subquadrate, 15–25 µm wide at the margin, 25–32 µm in the middle, with thickened walls and minute or missing trigones; cuticle covered with large papillae. *Underleaves* absent or present, large, abruptly long subulate from a short triangular base bearing 1–2 lanceolate or setaceous ciliae at margins. *Sterile* in Antarctica.

Taxonomic and nomenclatural notes. — The species was described by Montagne (1843) from specimens collected in the Strait of Magellan region during Dumont d'Urville's Antarctic voyage of 1837–1840 on the ships *Astrolabe* and *Zélée*. It was then transferred to *Chiloscyphus* by Gottsche *et al.* (1845) and retained in this genus until Persson and Grolle (1961) established a separate genus to accommodate it.

Differentiation. — A species characterised by its verrucose cuticle, bilobed leaves and long lanceolate-laciniate underleaves.

Reproduction in Antarctica. — Fertile plants unknown.

Habitat. — The only Antarctic specimen was collected on a 'north facing scree slope with *Polytrichum* sp. and *Chorisodontium aciphyllum*'. On mainland South America it grows commonly in the deciduous *Nothofagus* forests, and on the Falkland Islands in dwarf shrub heaths, less frequently on soil or rocks (Engel, 1990*a*).

World range. — A South American temperate species widely distributed but scattered in the *Nothofagus* zone at the western fringes of the continent, ranging from Tierra del Fuego to the Valdivian Province at lat. *ca* 40°S (Persson & Grolle, 1961). Additionally, it is known from the Falkland Islands (Engel, 1990*a*), South Georgia (Grolle, 1972*a*) and Elephant Island in Antarctica (Allison & Lewis Smith, 1973) (Fig. 59, inset).

Distribution in Antarctica. — Exceedingly rare, known from a single collection from Elephant Island in the South Shetland Islands archipelago (Fig. 59).

Specimens examined. — SOUTH SHETLAND ISLANDS. ELEPHANT ISLAND. 3.5 km east of Muckle Bluff, 153 m, *Allison 195* (AAS, KRAM).

Literature records. — SOUTH SHETLAND ISLANDS: Elephant Island (Allison & Lewis Smith, 1973: 187; Lewis Smith, 1979*a*: 235; Ochyra & Váňa, 1989*b*: 217).

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FIGURE 58. *Roivainenia jacquinotii*. **1**. Sterile shoots, lateral view. **2–6**. Leaves. **7–9**. Transverse section of leaves, note cuticular papillae. **10**. Transverse section of stem. **11–12**. Underleaves. **13**. Marginal cells in the median part of leaf. **14**. Basal cells in the middle part of leaf. **15**. Cells at leaf lobe. (All from *Allison 195*, AAS.) Scale bars: a – 1 mm (1) and 100 µm (7–8, 10–15); b – 100 µm (9); c – 1 mm (2–6).

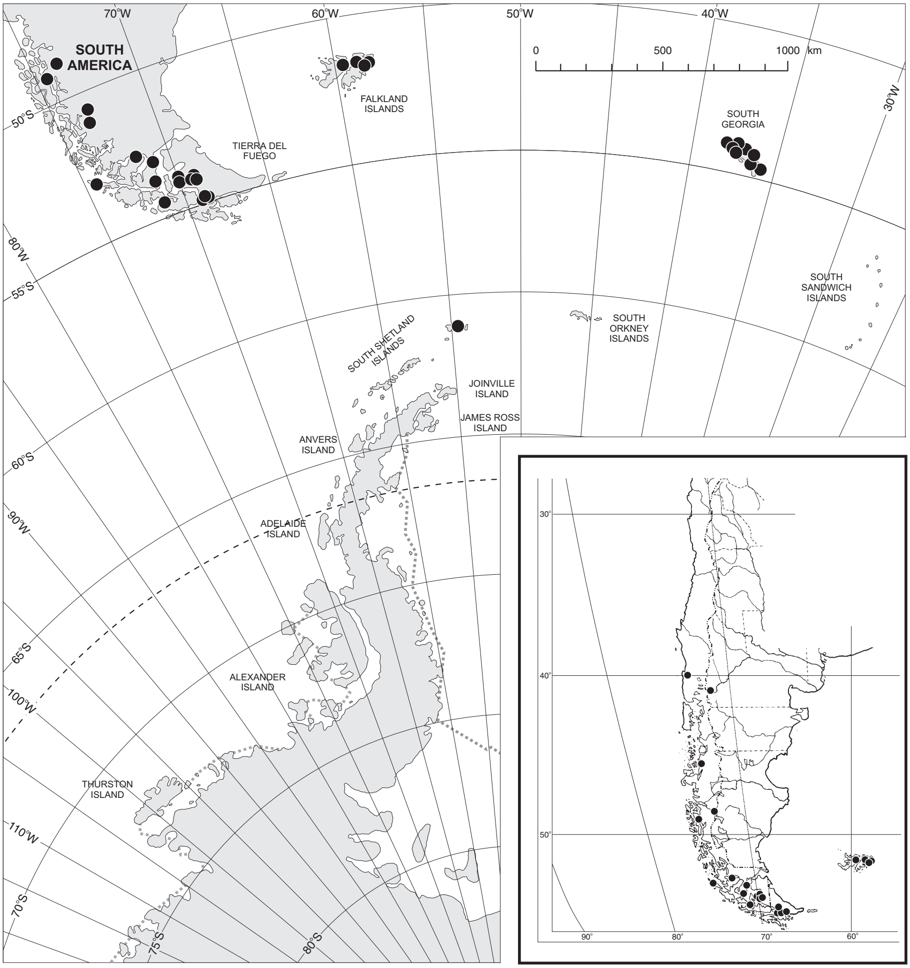

FIGURE 59. Distribution of *Roivainenia jacquinotii* in the Antarctic and Fuegian region. Inset: distribution in South America.

Family **VII. GYMNOMITRIACEAE** H. KLINGGR.

Gymnomitriaceae H. Klinggr., Höh. Crypt. Preuss.: 16. 1858 ["Gymnomitria"]. – TYPE: *Gymnomitrion* Corda em. Nees, *nom. cons*.

Plants very small to medium-sized, forming dense patches, mats or occasionally cushions, rarely intermixed in tufts of other bryophytes, green, greyish-green, silvery-grey to reddish-brown or blackish. *Stems* mostly erect or ascending, rarely creeping, firm, terete, without internal differentiation or rarely with hyalodermis; branching mostly lateral-intercalary (*Plagiochila*-type) or ventral-intercalary (*Bazzania*-type), terminal branches (*Frullania*-type) rare, stolons sometimes present. *Rhizoids* scattered or sometimes clustered on the ventral surface of the stem, never arising from leaf base, scarce. *Leaves* transversely or slightly succubously inserted, the insertion reaching across the stem midline (dorsally interlocking merophytes), unlobed to symmetrically bilobed, sometimes with decolorate apices or margins; leaf cells small to large, with thin or thick walls and with trigones; cuticle smooth to striate. *Underleaves* absent or occasionally vestigial. *Asexual reproduction* absent. *Dioecious* or *paroecious*. *Androecia* on main shoots, terminal, becoming intercalary, mostly spicate; male bracts similar to leaves, slightly concave; antheridia 1–4 per bract, with 2-seriate stalk. *Gynoecia* terminal, sometimes with subfloral innovations; female bracts similar to the leaves; bracteoles very rare (*Herzogobryum*). *Perianth* present or reduced. Perigynium present or absent. *Seta* relatively short, of numerous cell rows. *Capsule* mostly spherical, with 2(–3)-stratose wall; epidermal cells with nodular thickenings; inner cell walls with nodulose to semilunate thickenings. *Spores* smooth to finely granulate; elaters free, 2– or occasionally 3–4-spiral; spore/elater width ratio 2.0–2.5 : 1.

The Gymnomitriaceae are a small group consisting of 10–13 genera with some 75–80 species which are subdivided into two subfamilies, Gymnomitrioideae and Stephanielloideae (Váňa, 1999). The taxonomic position of some genera, including *Eremonotus*, *Lophonardia*, *Paramomitrion*, is still debatable and they possibly belong within other families. For example, *Eremonotus* representing the monotypic subfamily Eremonotoideae mentioned by Grolle (1983*a*) and Schuster (1996*b*) is very closely related to the genus *Anastrophyllum* of the Lophoziaceae. Members of this family can be recognised by more or less equally tri- or bilobed, rarely unlobed, concave and canaliculate leaves which are mostly transversely inserted and vertically oriented with entire or only crenulate margins. They do not produce gemmae, generally lack underleaves (although some primitive taxa have very small underleaves), possess 2–5 oil-bodies per cell in the mid-leaf and have dorsally interlocking merophytes.

Species of the Gymnomitriaceae are typically pioneer or early colonist plants which occur in montane or alpine as well as polar regions on bare ground to the margins of permanent snow or ice. The family is predominantly Northern Hemisphere in range where the most highly specialized taxa occur, but there are several primitive genera (*Acrolophozia*, *Herzogobryum*, *Nothogymnomitrion*) with an antipodal range. The latter suggest that the Gymnomitriaceae are probably derived from *Lophozia*-like ancestors (Schuster, 1996*b*).

Two species belonging within the antipodal genus *Herzogobryum* occur in the Antarctic.

1. HERZOGOBRYUM GROLLE

Herzogobryum Grolle, Rev. Bryol. Lichénol. **32**: 160. 1964 [“1963”]. – HOLOTYPE: *Herzogobryum cucullatum* (Herzog) Grolle (*Chondrophyllum cucullatum* Herzog).

Plants small, filiform, terete, in mats or compact tufts, greenish, greyish-green to brownish. *Stems* wiry, rigid, simple or lateral-intercalary to ventral-intercalary, very rarely terminally branched, in transverse section without differentiated cortex, composed of relatively large, thick-walled cells. *Rhizoids* scarce, scattered on the ventral surface of the stem, colourless. *Leaves* dense, sometimes scale-like at stem base and becoming continuously larger towards the stem apex, concave, subtransversely inserted, with dorsally interlocking merophytes, ovate to subrotundate, unlobed or bilobed to 0.1–0.2 of the length, unsitratose or partly bistratose in the lower half; margins often erose-denticulate with ± differentiated cells. *Dioecious*. *Antheridia* intercalary; male bracts leaflike, monandrous, antheridial stalk 1–2-seriate. *Gynoecia* terminal; female bracts gradually larger than the leaves, shallowly bilobed; bracteoles present, ovate to subulate, free or connected with one or both bracts. *Perianth* present, ovoid to ellipsoidal, contracted towards the plurilobulate mouth. *Perigynium* absent. *Seta* consisting of 8 larger external and 4 smaller internal cells. *Capsules* spherical, with 2-stratose walls. *Spores* finely granulate to smooth, brown, 9–14 µm in diameter; elaters bispiral, brown, 7–10 µm in diameter.

The genus *Herzogobryum* was established by Herzog (1952*b*) who called it *Chondrophyllum*. This name later proved to be an illegitimate homonym and Grolle (1963) introduced *Herzogobryum* as its replacement. Initially, the genus comprised a single species from Chile, *H. cucullatum* (Herzog) Grolle [=*H. vermiculare* (Schiffn.) Grolle] but Grolle (1966) in his monograph of this genus placed in it five species. Two further species were added to *Herzogobryum* later by Grolle (1975) and Schuster (1980*b*), namely *H. filarium* from Tasmania and *H. filiforme* from New Zealand, respectively. Schuster (1996*b*) reassessed the genus and transferred two species into separate genera, *Cephalomitrion* and *Nothogymnomitrion*, thus leaving the same number of species as proposed by Grolle (1966).

Herzogobryum is a strictly antipodal genus restricted to the Subantarctic and penetrating into the cool temperate zone at high elevation in New Zealand, Tasmania, Tristan da Cunha and southern South America (Schuster, 1969*c*, 1979*b*, 1982, 1983*b*). Two species of this genus extend to the Antarctic.

Key to the Antarctic species of *Herzogobryum*

1. Leaves slightly bilobed, strongly folded; leaf cells with the equally thickened cell walls and lacking trigones . . . . **1. *H. atrocapillum***
1. Leaves unlobed, concave; leaf cells with trigones . . . . **2. *H. teres***

1. ***Herzogobryum atrocapillum*** (Hook. f. & Taylor) Grolle Fig. 60

Herzogobryum atrocapillum (Hook. f. & Taylor) Grolle, Oesterr. Bot. Zeitschr. **113**: 228. 1966. – *Gymnomitrion atrocapillum* Hook. f. & Taylor *in* Taylor, London J. Bot. **5**: 258. 1846. – *Jungermannia atrocapilla* (Hook. f. & Taylor) Hook. f. & Taylor *in* Hook. f., Fl. Antarct. **2**: 423. 1847. – *Cesia atrocapilla* (Hook. f. & Taylor) Mitt., Phil. Trans. Roy. Soc. London **168**: 43. 1879. – *Cesiusa atrocapilla* (Hook. f. & Taylor) Kuntze, Revisio Gen. Plant.: 843. 1891. – *Acolea atrocapilla* (Hook. f. & Taylor) Steph., Sp. Hepat. **2**: 4. 1901. – Type: On clay, at an elevation of 600 feet, Foul Haven, Kerguelen's Land, May 1840, Dr. Joseph D. Hooker [Lectotype: FH-taylor!; isotypes: BM-hook!, NY!, W-lindenberg!].

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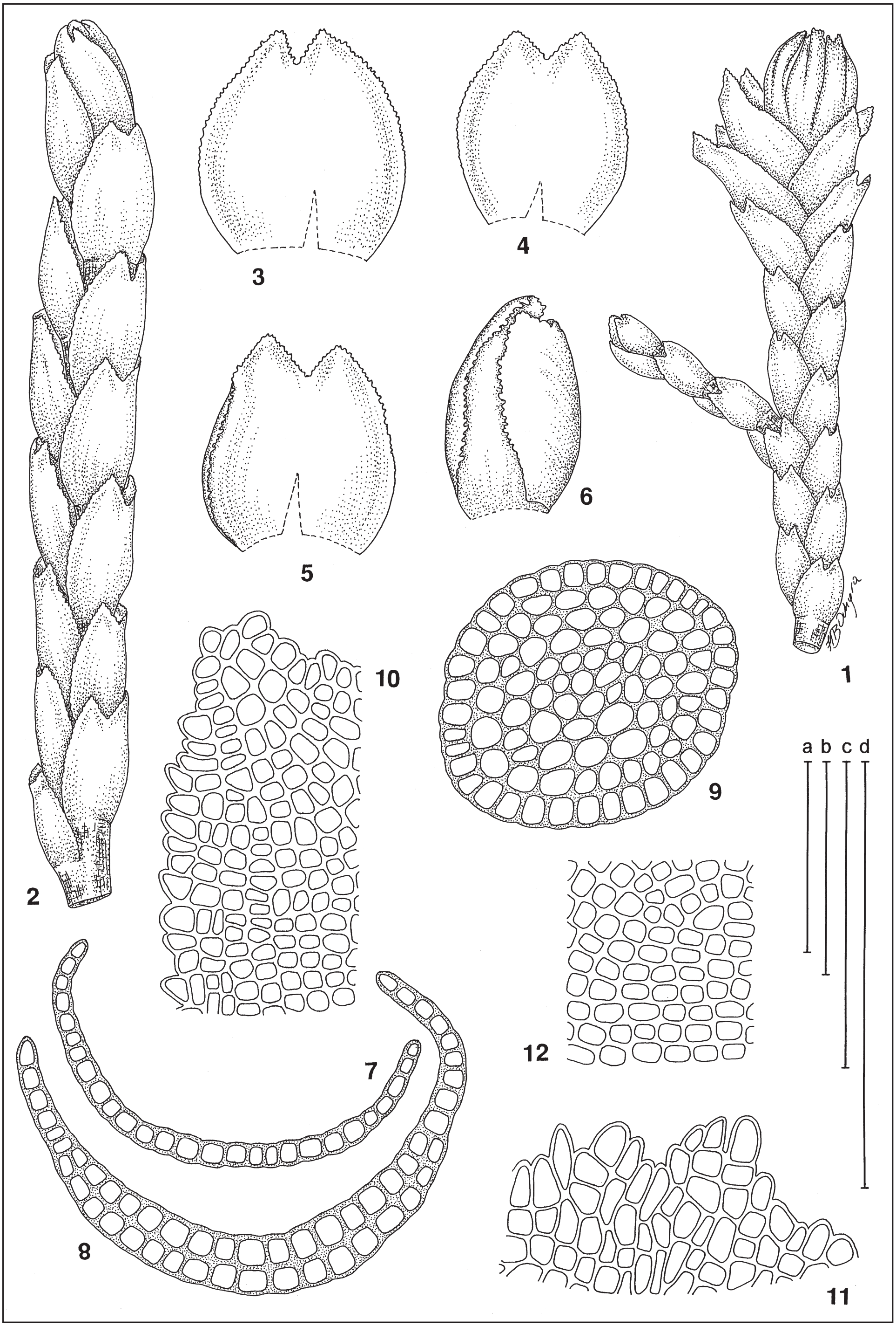
Figure 60. *Herzogobryum atrocapillum*. **1**. Apex of gynoecial branch, with mature perianth. **2**. Sterile shoot. **3–6**. Leaves. **7–8**. Transverse sections of leaves. **9**. Transverse section of stem. **10**. Lobe and upper marginal leaf cells. **11**. Cells at perianth mouth. **12**. Cells from middle of perianth. (All from *Lewis Smith 5441B*, AAS.) Scale bars: a – 100 µm (7–12); b – 1 mm (1); c – 0.5 mm (3–6); d – 1 mm (2).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Plants very small, filiform, interwoven, creeping or ascending, reddish-brown or blackish, often becoming whitish because of the hyaline leaf margins. *Stems* simple, 3–12 mm long, rigid, julaceous, simple or lateral-intercalary branched, in transverse section 8–12 cells in diameter, with cortical cells firm-walled, hardly differentiated, surrounding slightly larger, thick-walled and rigid medullary cells. *Rhizoids* scattered, relatively rare. *Leaves* densely imbricate, mostly transversely inserted, strongly concave-folded to keeled, shallowly bilobed to 0.1–0.2 of the length to emarginate, in transverse section bistratose below in the median part; lobes short, triangular; marginal leaf cells thin-walled, bleached, 8–12 × 14–25 µm, radially elongate, forming a crenulate leaf border; mid-leaf cells with thick, brownish to reddish walls, without trigones, 10–15 × 13–18(–20) µm; cuticle smooth. *Underleaves* absent. *Remainder* unknown in Antarctica.

Taxonomic and nomenclatural notes. — *Herzogobryum atrocapillum* was the earliest species named in this genus. It was described by Taylor (1846) as *Gymnomitrion atrocapillum* from material collected by J. D. Hooker on Îles Kerguelen during his Antarctic voyage on the ships *Terror* and *Erebus* commanded by James C. Ross. It was subsequently transferred to other genera including the all-encompassing *Jungermannia* (Taylor & Hooker, 1847), *Cesia* (Mitten, 1879) and *Acolea* (Stephani, 1906). However, only a very limited number of specimens of this species is known due to difficult access to subantarctic islands, and consequently its name has only one heterotypic synonym, *Gymnomitrion marionense* used by Arnell (1953) for plants collected on Marion Island.

Differentiation. — It is unlikely to be confused with other liverworts, except for other species of *Herzogobryum*. It is distiguished from *H. teres* by its slightly bilobed and strongly folded leaves with equally thickened cell walls which lack the trigones.

Reproduction in Antarctica. — Fertile plants unknown.

Habitat. — In wet rock crevices and on wet, peaty soil covering basaltic gravel associated with crustose lichens (*Pannaria hookeri* and *Psoroma hypnorum*) and also growing on necrotic cushions of *Dicranoweisia brevipes* and in tufts of *Andreaea gainii*, usually in communities of the fruticose lichen and moss cushion subformation.

World range. — A circumsubantarctic species occurring on South Island, New Zealand (Schuster, 1996*b*), Heard Island (Bergstrom & Selkirk, 1997), Îles Kerguelen (Taylor, 1846; Grolle 1966; Schuster, 1996*b*), Îles Crozet (Schuster, 1996*b*), Marion Island (Arnell, 1953; Grolle, 1971*a*; Gremmen, 1982; Schuster, 1996*b*) and Prince Edward Island (Schuster, 1996*b*) and from the Antarctic (Fig. 61). Formerly, *Herzogobryum atrocapillum* was considered as an amphiatlantic subantarctic species (Ochyra & Váňa, 1989*b*) but the recent discovery of this species in New Zealand changed its phytogeographical status, and now it must be considered as a circumsubantarctic species.

Distribution in Antarctica. — An apparently very rare species, known only

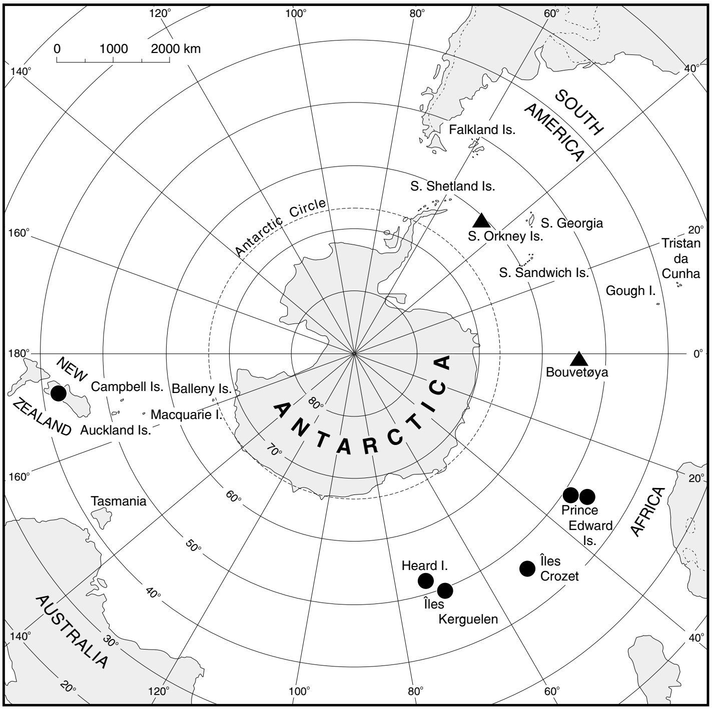


FIGURE 61. Global distribution of *Herzogobryum atrocapillum*. The Antarctic localities are indicated by triangles.

from the isolated island of Bouvetøya (Bell & Blom, 1986) and Signy Island in the South Orkney Islands (Fig. 61).

Specimens examined. — BOUVETØYA. Moseryggen, summit ridge, 270 m, *Engelskjøn 44 & 399* (BG) and 295 m, *Engelskjøn 49.1 & 49.3* (BG); same locality, south-easternmost shelf, *Engelskjøn 310* (BG); Rustadkollen, *Engelskjøn 250* (BG).

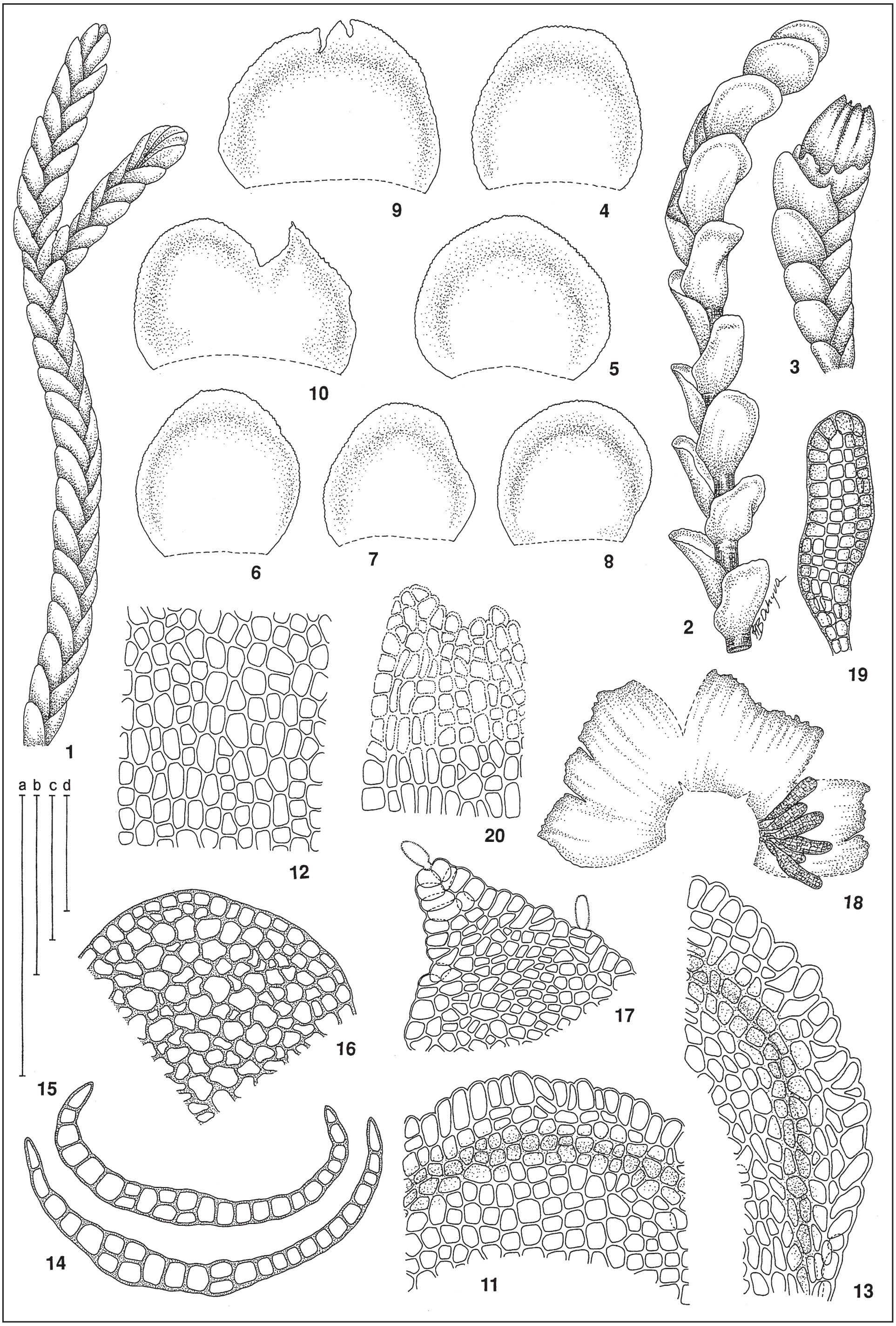
SOUTH ORKNEY ISLANDS. SIGNY ISLAND. Moraine Valley, west side of Rusty Bluff, 50 m, *Lewis Smith 541B* (AAS, KRAM); cliffs above Paal Harbour, *Lewis Smith 1449* (AAS, KRAM).

Literature records. — BOUVETØYA: Moseryggen and Rustadkollen (Bell & Blom, 1986: 12; Engelskjøn & Jørgensen, 1986: 74; Engelskjøn, 1987: 145, 161; Ochyra & Váňa, 1989*b*: 217).

2. *Herzogobryum teres* (CARRINGTON & PEARSON) GROLLE FIG. 62

Herzogobryum teres (Carrington & Pearson) Grolle, Oesterr. Bot. Zeitschr. **113**: 223. 1966. – *Jungermannia teres* Carrington & Pearson, Pap. Proc. Roy. Soc. Tasmania **1887**: 9, *p. 42, f. 1–16*. 1888. – *Jamesoniella teres* (Carrington & Pearson) Steph., Sp. Hepat. **2**: 100. 1901. – TYPE: Hab., near top of Mt. Wellington, December 25th, 1885. 275 [HOLOTYPE: MANCH (*non vidi*); ISOTYPE: G!].

Plants small to medium-sized, in loose to compact, sometimes cushion-like turfs, or in thin mats, somewhat glossy, usually dark coloured, almost black or blackish-green when fresh, green, yellowish-green to slightly dull reddish at least above but with decolorate leaf margins on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drying. *Stems* terete, julaceous, wiry, rather rigid and stout, simple or lateral-intercalary to, rarely, ventral-intercalary branched, in transverse section 10–15 cells in diameter, consisting of a poorly differentiated cortex of slightly smaller, thicker-walled cells in 1–3 rows surrounding medullary cells with markedly incrassate and collenchymatous cells. *Rhizoids* scarce, scattered. *Leaves* contiguous to weakly or moderately closely imbricate, succubously inserted, concave, saucer-shaped, orbicular to ovate, broadly inserted on the stem, to 0.35–0.4 mm long, 0.45–0.5 mm wide, unistratose or partially bistratose in median and basal parts; marginal leaf cells radially elongate, thin-walled, mostly decolorate, 10–15 × 25–30 μm, erose with age, forming a distinct, crenulate 1–4-seriate border; inner leaf cells slightly thick-walled, with small trigones, 15–20 × 15–25 μm; cuticle smooth or faintly striolate. *Underleaves* rare, small, lanceolate, crenulate, united with one lateral leaf. *Dioecious*. *Androecia* becoming intercalary, short; male bracts monandrous, antheridial stalk biseriate. *Gynoecia* terminal; female bracts larger than the leaves, shallowly bilobed, dentate to lobulate; bracteoles ovate-lanceolate, free. *Perianth* (only young found) ovoid, pluriplicate, polystratose basally. *Sporophytes* unknown in the Antarctic.

Taxonomic and nomenclatural notes. — This species was originally described from Tasmania as *Jungermannia teres* (Carrington & Pearson, 1888) but, apart from the present generic placement, it was also positioned in *Jamesoniella* (Stephani, 1906). Despite its wide range and broad variation, the species was correctly interpreted by hepaticologists, so only three heterotypic synonyms of its name are available (Grolle, 1966; Schuster, 1996*b*).

Differentiation. — A colourless marginal border seperates *Herzogobryum teres* from all other Antarctic hepatics with unlobed leaves, except for other species of this genus. However, unlobed, deeply concave and saucer-shaped leaves give the plants a characteristic appearance and immediately distinguish it from *H. atrocapillum* and other liverworts.

Reproduction in Antarctica. — Fertile plants unknown.

Habitat. — It usually grows on permanently moist to wet gravelly soil, especially in late snow patches, and on wet soil over rock ledges, often in association with *Andreaea* spp., *Anthelia juratzkana*, *Pachyglossa dissitifolia* and *Sanionia georgico-uncinata*. It occasionally occurs in shaded rock crevices or on pockets of soil and gravel amongst loose stones.

World range. — A circumsubantarctic species and the commonest and most widespread within the genus. It occurs at high elevations in New Zealand (North and South Islands), on Tasmania, Marion Island, Tristan da Cunha and in southern

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FIGURE 62. *Herzogobryum teres*. **1–2**. Sterile shoots, dorso-lateral aspect. **3**. Apex of gynoecial branch, with mature perianth. **4–8**. Leaves. **9–10**. Outer female bracts. **11**. Distal leaf cells. **12**. Mid-leaf cells. **13**. Basal leaf cells at margin. **14–15**. Transverse sections of leaf. **16**. Transverse section of stem. **17**. Lobe cells of outer female bract. **18**. Innermost female bracts, with archegonia. **19**. Archegonium. **20**. Cells at perianth mouth. (1, 3, 9–10, 12–15, 17–20 from *Ochyra 2014/*80; 2, 4–8, 11, 16 from *Ochyra 2498/80*, KRAM.) Scale bars: a – 1 mm (4–10, 18); b – 1 mm (2); c – 1 mm (3); d – 1 mm (1) and 100 μm (11–17, 19–20).

South America, including the Falkland Islands and South Georgia[2] (Schuster, 1969*c*, 1979*b*, 1983*b*; Engel, 1990*a*) (Fig. 63).

Distribution in Antarctica. — The species is locally frequent and abundant on Bouvetøya as well as on the South Orkney Islands and South Shetland Islands, with two isolated stations on the Graham Coast on the west Antarctic Peninsula, including Cape Tuxen (lat. 65°16’S) and Takaki Promontory (lat. 65°33’S). It prefers elevated areas and frequently it is found from 100–300 m altitude, but attaining 600 m at its southernmost site (Fig. 64).

Specimens examined. — BOUVETØYA. Moseryggen, summit ridge, 260 m, *Engelskjøn 291*(BG), 275 m, *Engelskjøn 213* (BG) and 287 m, *Engelskjøn 396* (BG).

SOUTH ORKNEY ISLANDS. **CORONATION ISLAND**. Olivine Point, *ca* 35 m, *Lewis Smith 146* (AAS, KRAM); moraine below Windscoop Buttress on east side of Sunshine Glacier, *ca* 175 m, *Webb 150B* (AAS, KRAM). **MATTHEWS ISLAND**. North-west coast, 50 m, *Lewis Smith 163* (AAS, KRAM). **POWELL ISLAND**. South-east coast, *ca* 135 m, *Lewis Smith 197D & 199* (AAS, KRAM); middle of east coast, *ca* 135 m, *Lewis Smith 226* (AAS, KRAM); promontory west of John Peaks, *ca* 65 m, *Lewis Smith 261* (AAS, KRAM); west coast, 300 m, *Lewis Smith 239B* (AAS, KRAM). **SIGNY ISLAND**. West of the col between Jane Peak and Snow Hill, 150 m, *Longton 1199* (AAS, KRAM); ridge north of Jane Peak, *ca* 165 m, *Holdgate 764B* (AAS, KRAM); between Jane Peak and Knob Lake, 50 m, *Lewis Smith 10798* (AAS, KRAM); Gneiss Hills, 200 m, *Lewis Smith 8113* (AAS, KRAM); Moraine Valley, *Lewis Smith 1842* (AAS, KRAM); east side of Moraine Valley, towards northern end, *ca* 35 m, *Longton 1090* (AAS, KRAM); Moraine Valley, 60 m, *Lewis Smith 5223* (AAS, KRAM), 75 m, *Lewis Smith 10850* (AAS, KRAM) and *ca* 80 m, *Lewis Smith 5226*; Garnet Hill, 100 m, *Lewis Smith 5204* (AAS, KRAM); Factory Bluffs, 100 m, *Lewis Smith 7007* (AAS, KRAM); plateau between Observation Bluff and Factory Bluffs, 85 m, *Lewis Smith 5229* (AAS, KRAM); south-west shore of Factory Cove, *ca* 50 m, *Longton 1078* (AAS, KRAM); Factory Cove, slopes behind Base, *ca* 35 m, *Holdgate 745* (AAS, KRAM); Factory Cove, top of hill behind Base, *ca* 50 m, *Lewis Smith 853* (AAS, KRAM). **MOE ISLAND**. Near summit, 200 m, *Lewis Smith 5243A* (AAS, KRAM).

SOUTH SHETLAND ISLANDS. **KING GEORGE ISLAND**. ***Admiralty Bay***: The Tower, 365 m, *Ochyra 1378/80* (KRAM, PRC); Creeping Slopes, 135 m, *Ochyra 1274/80* (KRAM, PRC); Italia Valley, 100 m, *Ochyra 88/80 & 122/80* (AAS, KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 24]; Komandor Peak, 230 m, *Ochyra 1965/80* (KRAM, PRC) and 250 m, *Ochyra 1936/80* (AAS, KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 50];

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[2] Hitherto, *Herzogobryum teres* has not been recorded from South Georgia, although it is scattered throughout the island as evidenced by many specimens preserved in AAS. Some representative specimens are cited here to document the occurrence of this species there. **SOUTH GEORGIA**: Bird Island, east of Jordan Cove, Bird Island, 65–135 m, *Bell 1037* (AAS); same locality, Gazella Peak, *ca* 165 m, *Greene 371B, 372C, 374C & 393C* (AAS); same locality, Roché Peak, *ca* 300 m, *Greene 434* (AAS) and *ca* 400 m, *Greene 1163A* (AAS); Bay of Isles, Paul Beach, northern peak of Murphy Wall, *ca* 335 m, *Greene 1186C* (AAS); Barff Peninsula, Sandebugten, *ca* 15 m, *Greene 555A* (AAS); Undine Harbour, between isthmus and lower glacial plain of Hope Valley, *Greene 690E* (AAS); same locality, Lower glacial plain, Hope Valley, *Greene 715A, 751D & 752C* (AAS); Cumberland East Bay, north-west of Grytviken, to east of snout of Hodges Glacier, *ca* 415 m, *Greene 1808B* (AAS).

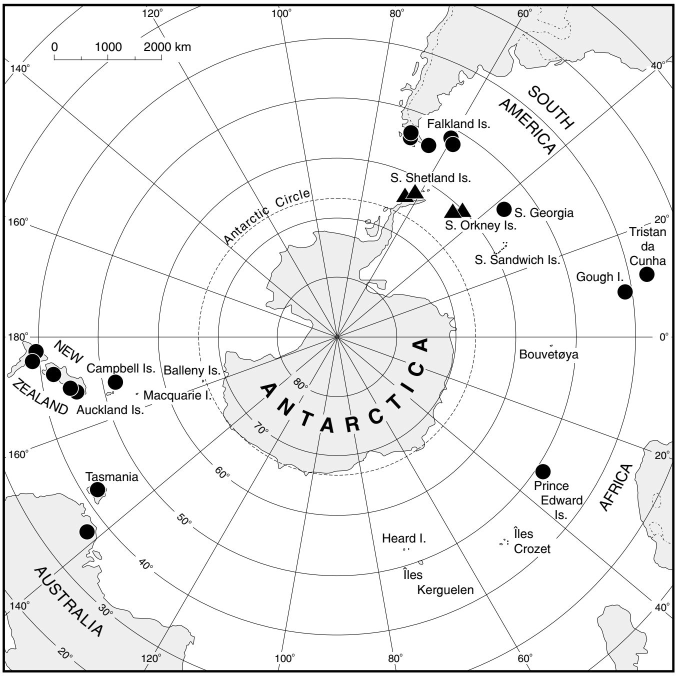


FIGURE 63. Global distribution of *Herzogobryum teres*. The Antarctic localities are indicated by triangles.

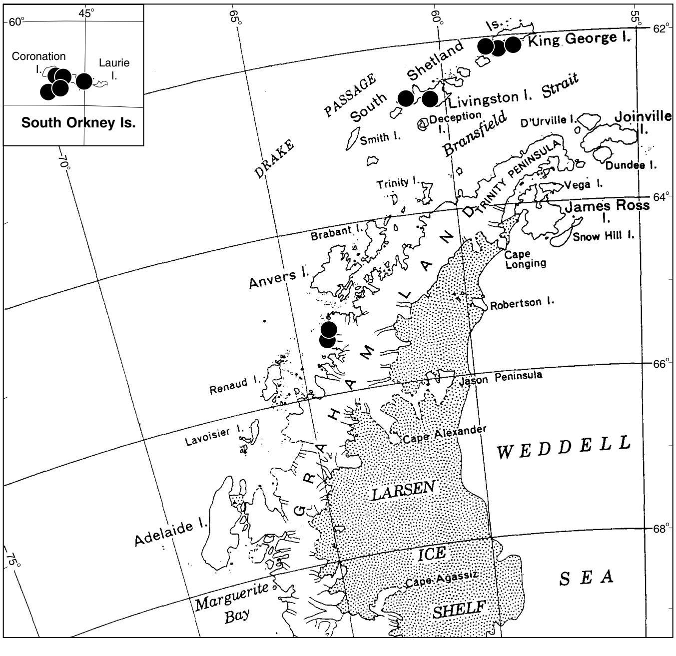


FIGURE 64. Distribution of *Herzogobryum teres* in the maritime Antarctic.

Kapitan Peak, 190 m, *Ochyra 1910/80* (KRAM, PRC) and 210 m, *Ochyra 1907/80* (KRAM, PRC); Wegger Peak, 290 m, *Ochyra 2008A/80* (KRAM, PRC) and 300 m, *Ochyra 2010/80* [*Bryophyta Antarctica Exsiccata* No. 150] *& 2014/80* (AAS, KRAM, PRC); Speil Point, 3 m, *Ochyra 602/80* (KRAM, PRC); British Point, 50 m, *Ochyra 557/80* (KRAM, PRC); Bell Zygmunt, 300 m, *Ochyra 2683/80* (KRAM, PRC). ***Barton Peninsula***: Winship Point, 5 m, *Jabłoński 194* (KRAM). ***Marian Cove***. North Spit, *Lindsay 781* (AAS, KRAM). ***Fildes Peninsula***: Suffield Point, 20 m, *Ochyra 2450/80* (KRAM, PRC); Ardley Island, 5 m, *Ochyra 2498/80* [*Bryophyta Antarctica Exsiccata* No. 23] *& 2499/80* (AAS, KRAM, PRC); without specific locality, 14 Jan 1989, *Li BA10 & BA21* (AAS). LIVINGSTON ISLAND. ***Byers Peninsula***: Clark Nunatak, 180, *Lindsay 218 & 224B* (AAS, KRAM). ***Hurd Peninsula***: South Bay, Mt. Reina Sofia, 245 m, *Schulz 76* (Hb. Schulz, KRAM).

WEST ANTARCTIC PENINSULA. GRAHAM COAST. Cape Tuxen, Mt. Demaria, 250–300 m, *Lewis Smith 4918* (AAS, KRAM) and 600 m, *Fowbert 9* (AAS, KRAM) and *Lewis Smith 10652* (AAS, KRAM). ***Grandidier Channel***: second largest island of Takaki Promontory, 10–35 m, *Lewis Smith 4367* (AAS, KRAM).

Literature records. — BOUVETØYA: Moseryggen (Bell & Blom, 1986: 12; Engelskjøn & Jørgensen 1986: 74; Engelskjøn 1987: 145, 161; Ochyra & Váňa, 1989*b*: 218). SOUTH ORKNEY ISLANDS: Coronation Island (Ochyra & Váňa, 1989*b*: 218); Lynch Island (Bonner & Lewis Smith, 1985: 82); Powell Island (Bonner & Lewis Smith, 1985: 91; Ochyra & Váňa, 1989*b*: 218); Signy Island (Lewis Smith, 1972: 19; 1987: 242; Lewis Smith & Gimingham, 1976: 36; Lewis Smith & Coupar, 1986: 194; Ochyra & Váňa, 1989*b*: 218); Moe Island (Bonner & Lewis Smith, 1985: 68). SOUTH SHETLAND ISLANDS: King George Island (Ochyra *et al.*, 1982: 261; Ochyra & Váňa, 1989*a*: 204; 1989*b*: 218; Myrcha *et al.*, 163; Chen *et al.*, 1993: 50; 1995: 136–137 & 142–144 both as *Gymnomitrion corallioides* and *Odontoschisma macounii*; Okada & Kanda, 1994: 58; Schuster, 1996*b*: 35; Li *et al.*, 1998*a*: 201 as *Gymnomitrion corallioides* and *Odontoschisma macounii*; 1998*b*: 225 as *Gymnomitrion* sp.; 1998*c*: 233 as *Gymnomitrion corallioides*); Livingston Island (Sancho *et al.*, 1999: 322).

GYMNOMITRIACEAE SPECIES EXCLUDED FROM ANTARCTICA

Marsupella boeckii (Austin) Lindb. — This species was reported from Fildes Peninsula on King George Island, South Shetland Islands, by Chen *et al.* (1995) but the voucher specimen represents *Lophozia excisa*.

Gymnomitrion corallioides Nees. — This species was reported from Fildes Peninsula on King George Island, South Shetland Islands, by Chen *et al.* (1995) but the voucher specimen represents *Herzogobryum teres*.

Family VIII. SCAPANIACEAE MIG.

Scapaniaceae Mig., Krypt.-Fl. Deutschl. **1**: 479. 1904. – TYPE: *Scapania* (Dumort.) Dumort., *nom. cons.*

Plants small to large and robust, green, yellowish-green to reddish, brownish or purplish. *Stems* prostrate to ascending, simple or terminal-intercalary (*Frullania*-type) to lateral-intercalary (*Plagiochila*-type) branched, with 1–3(–5)-stratose cortex of smaller, thick-walled cells and frequent fungal hyphae, sometimes appearing with age. *Rhizoids* usually abundant, scattered on the postical surface of stem, hyaline, pale yellow or brown. *Leaves* succubous, horizontal, conduplicate-bilobed, with the lobes separated by bluntly or sharply defined keel and the ventral lobe at least slightly larger than the dorsal lobe; leaf margins entire or toothed; leaf cells thin-walled to ± collenchymatous, with granulate oil-bodies, usually 2–15 per cell. *Underleaves* absent. *Gemmae* almost always present at the apices of the uppermost leaves, 1–2(–5)-celled. *Monoecious* (paroecious or autoecious) or more commonly *dioecious*. *Male inflorescences* terminal or intercalary, formed of some pairs of male bracts saccate at base; antheridia mostly 2–4 per bract, antheridial stalk uniseriate. *Gynoecia* terminal; female bracts similar to the leaves, slightly larger and ± saccate; bracteoles absent. *Perianth* dorsiventrally flattened (except for some primitive taxa), with a wide, not contracted mouth. *Seta* composed of numerous undifferentiated rows of cells. *Capsule wall* (3–)4–6(–7)-stratose. *Spores* minutely papillose; elaters (1–)2-spiral; spore/elater width ratio 1–3 : 1.

The Scapaniaceae are one of the larger and taxonomically not definitely clarified families. It is related to the Lophoziaceae with which it shares a number of characters including similarly inserted, bilobed leaves with the dorsal lobe tending to be smaller than the ventral lobe, abundant production of the gemmae and their form, terminal perianth, multistratose capsule wall, and lateral branching. However, they differ in several advanced characters including the presence of the keel between the leaf lobes, toothed leaf margins and dorsiventrally flattened perianth.

Grolle (1983*a*) placed in the Scapaniaceae seven genera divided into four subfamilies. However, in recent studies Schuster (1999) considered two of them to be discordant elements in the Scapaniaceae and recognised them as families in their own right, the monotypic Delavayellaceae and the Blepharidophyllaceae with three genera (*Blepharidophyllum*, *Cladnarium* and *Krunodiplophyllum*). Additionally, Potemkin (1999) segregated the genera *Diplophyllum* and *Douinia* into the separate family Diplophyllaceae and merged *Macrodiplophyllum* with *Scapania*. If these novelties are accepted, the Scapaniaceae become monotypic. The family is predominantly Holarctic in range, and in the Antarctic it is represented by two species of the cosmopolitan genus *Scapania*.

1. SCAPANIA (DUMORT.) DUMORT.

Scapania (Dumort.) Dumort., Recueil Observ. Jung.: 14. 1835, *nom. cons.* – *Radula* Dumort. sect. *Scapania* Dumort., Sylloge Jung. Eur. Indig.: 38. 1831. – TYPE (*cons.*): *Scapania undulata* (L.) Dumort. (*Jungermannia undulata* L.).

Plants very small, small to large, ranging from 0.5 to 25 cm, in flat patches, loose or dense mats or turfs or scattered amongst other bryophytes, pale green, reddish-brown to purplish. *Stems* mostly prostrate, rarely ascending or erect, often with deflexed apices, simple or infrequently with lateral-intercalary or terminal branches, with or without differentiated cortex, often mycorrhizal. *Rhizoids* usually abundant, scattered on the ventral surface of stem. *Leaves* succubously oblique or transversely inserted, conduplicate, bilobed, usually keeled, with a weak or sharp keel of varying length, 0.1–0.8 the length of the whole leaf, winged or not; dorsal lobe mostly lying on and always smaller than the ventral lobe; leaf lobes of different form, widely ovate, cordate to ovate, not ligulate; leaf margins entire or dentate with mostly sharp teeth, decurrent or not; leaf cells thin-to thick-walled, not to strongly collenchymatous. *Underleaves* absent or very rudimentary. *Gemmae* 1–2(–5) celled, mostly ovate, rarely angulate. *Dioecious*, rarely *paroecious*. *Male bracts* in 3–15 pairs; antheridia intercalary, saccate at base. *Gynoecia* terminal; female bracts larger than the leaves, slightly saccate. *Perianth* dorsiventrally flattened, with a wide, truncate, entire to dentate or ciliate mouth. *Capsule* ovoid, with 3–7-stratose wall. *Spores* small, 8–20 µm in diameter; elaters 2-spiral; spore/elater width ratio 1.3–1.7(–2) : 1.

Scapania is a relatively large genus with about 110 recognised species, many of which are conspecific with others or still in need of reduction, so the final number may be reduced by at least 50%. Müller (1905) produced a global monograph of the genus, and some regional revisions are also available, for example for northern Eurasia (Buch, 1922, 1928) and eastern North America (Schuster, 1974), but the earlier pair are largely out-of-date. The genus needs careful revision, especially at species level, and the recent studies by Potemkin (1994, 1998, 1999) focus mainly on suprageneric classification and evolution of the genus.

Normally, *Scapania* does not pose problems with recognition as a genus, and its conduplicate-bilobed leaves and strongly dorsiventrally compressed perianth are very characteristic. However, in some primitive species the leaves have no sharply defined keel and consequently they are not obviously conduplicate, resembling the leaves of the Lophoziaceae.

Scapania is essentially a subcosmopolitan genus but with a major concentration of species in the Northern Hemisphere. Beyond the Holarctic species of this genus are restricted in occurrence to high elevations in tropical mountains and/or temperate zone in the austral region, including four species in Central and South America, two in Africa, five in Australasia, one in New Caledonia and one in the Pacific region (Samoa) (Váňa, 1999). Two species are exceedingly rare and localised in Antarctica. They are recognised in the following key.

KEY TO THE ANTARCTIC SPECIES OF *SCAPANIA*

1. Leaves subequally bilobed, with ± squarrose lobes and moderately sharp keel; leaf cells thick-walled, with small trigones; marginal 2–4 rows of cells with more thick-walled cells, differentiated as ± well-defined border . . . . **1. *S. gamundiae***
1. Leaves not subequally bilobed, with weakly defined keel (often *Lophozia*- rather than *Scapania*-like); leaf cells thin-walled, with trigones; marginal rows of cells undifferentiated . . . . **2. *S. obcordata***

1. ***Scapania gamundiae*** R. M. SCHUST. FIG. 65

Scapania gamundiae R. M. Schust., Bull. Nat. Sci. Mus. Tokyo **11**(1): 14, *f. 1*. 1968. – TYPE: Argentina, Tierra del Fuego: Cerro Garibaldi, SE of Lago Escondido, near Rte 3 between Ushuaia and Rio Grande, in rather dry crevices of cliff face, near persistent ice patches, ca. 900 m, 26 Feb 1961, *R. M. Schuster & I. Gamundi de Amos 58305* [HOLOTYPE: Hb. Schuster (*non vidi*); ISOTYPE: TNS (*non vidi*)].

Plants small forming small patches, yellowish-green, becoming bronzed with age. *Stems* prostrate to ascending, 4–10 mm long, 0.8–1.4 mm wide, simple to sparingly lateral-intercalary branched, in transverse section 13–15 cells in diameter, with a strongly differentiated cortex of 1–3 rows of cells with incrassate, brownish walls surrounding thin-walled, slightly collenchymatous medullary cells, strongly mycorrhizal with age, many of which becoming brown and filled with hyphae. *Leaves* dense, concave, orbicular to broadly orbicular, slightly subequally bilobed to 0.1–0.2 the length, imperfectly conduplicate with a weak keel; lobes concave, not or very slightly decurrent, edentate, with the apices drawn out as a large-celled angular extension developing gemmae; leaf cells thick-walled, with small trigones; marginal cells in 3–4 rows with strongly thickened walls, 14–18 µm wide, some cells tangentially elongate, forming a distinct border; median cells 20–25 µm in diameter, some basal cells short-rectangular to 30 µm; apical cells of the lobe apices tangentially elongated to 20–25 µm. *Gemmae* commonly produced on angular extensions of the lobes, 2-celled, brownish, ovoid to fusiform, 12–15 × 20–23 µm. *Sterile*.

Taxonomic and nomenclatural notes. — *Scapania gamundiae* was only recently described from a single collection Tierra del Fuego by Schuster (1968*b*). The Antarctic material differs from the Fuegian type in two respects, namely in the sharply differentiated cortex and the presence of gemmae. Schuster (1968*b*) was uncertain of the true affinity of this species and drew attention to some characters which made it close to species of three subgenera, namely subgen. *Scapania*, subgen. *Scapaniella* and subgen. *Buchiella*. The perfectly developed cortex as well as the shape of the gemmae clearly confirm the alliance of *S. gamundiae* with *S. cuspiduligera* from subgen. *Scapaniella*, and definitely preclude its relationship to subgen. *Buchiella* which could eventually be evident on the basis of the stem anatomy of the Fuegian material. *S. gamundiae* seems to be a distinct species of subgen. *Scapaniella* which differs from all other species in its broadly rounded, subequal leaf lobes and more distinct keel of the leaves.

Differentiation. — In the Antarctic *Scapania gamundiae* is unlikely to be mistaken for any other liverwort species since it is the only species having distinctly keeled leaves. The differences with *S. obcordata* are discussed under this species.

Reproduction in Antarctica. — Like the Fuegian type, the Antarctic population is sterile, but gemmae are copiously formed at apices of leaf lobes, enabling vegetative reproduction.

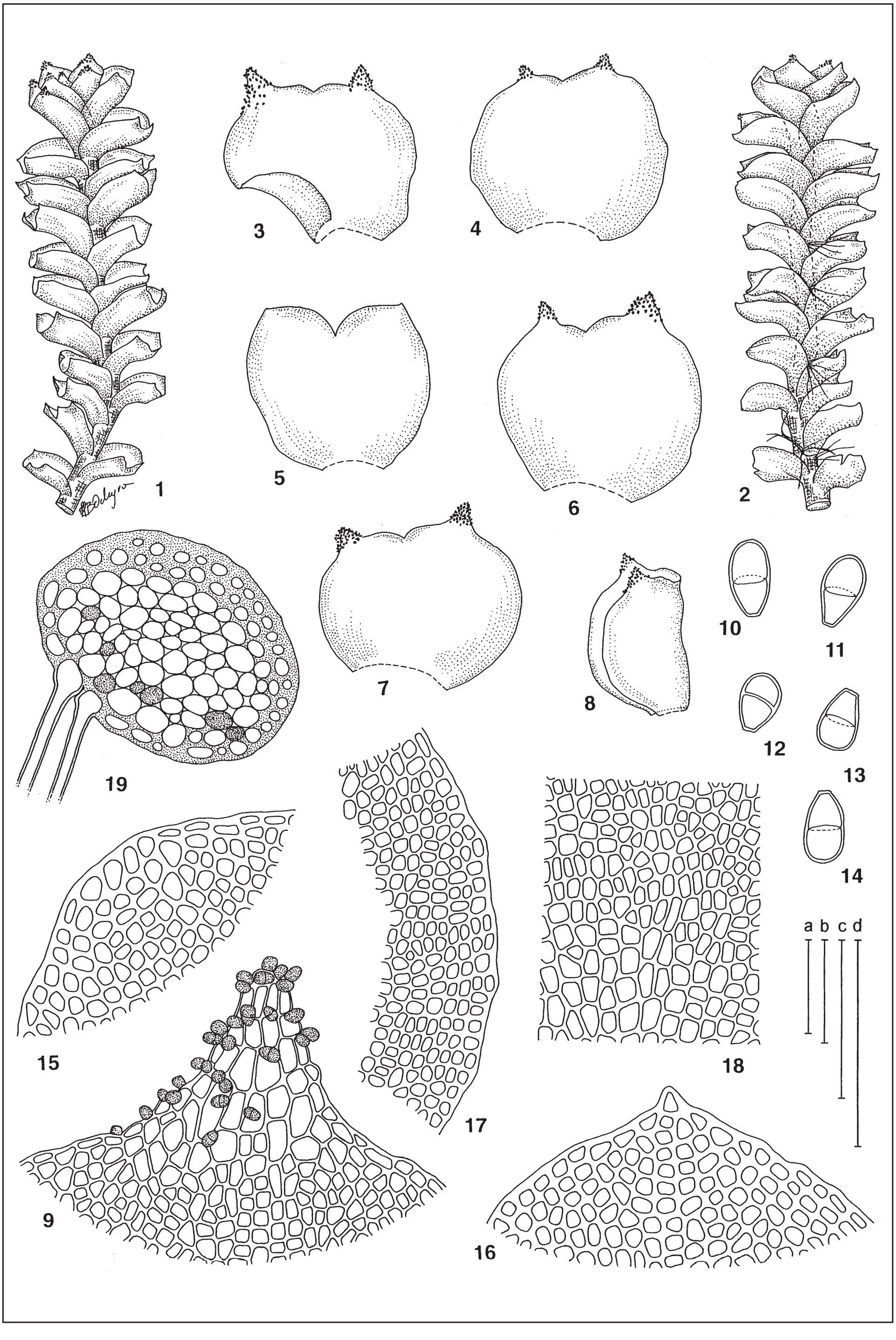
Habitat. — The specimen of this species occurred in a damp rock crevice in a steep rock face amongst *Pohlia cruda* and *Platydictya jungermannioides* in association with *Anthelia juratzkana* and *Cephaloziella varians*.

World range. — A Fuegian-Antarctic species known only from the type collection on Isla Grande de Tierra del Fuego and from a single station in Antarctica (Fig. 66).

Distribution in Antarctica. — The species is known from a single collection on Signy Island, and is here reported for the first time from Antarctica (Fig. 66).

Specimens examined. — SOUTH ORKNEY ISLANDS. SIGNY ISLAND. Above Paal Harbour, *ca* 85 m, *Lewis Smith 682* (AAS, KRAM).

Literature records. — None.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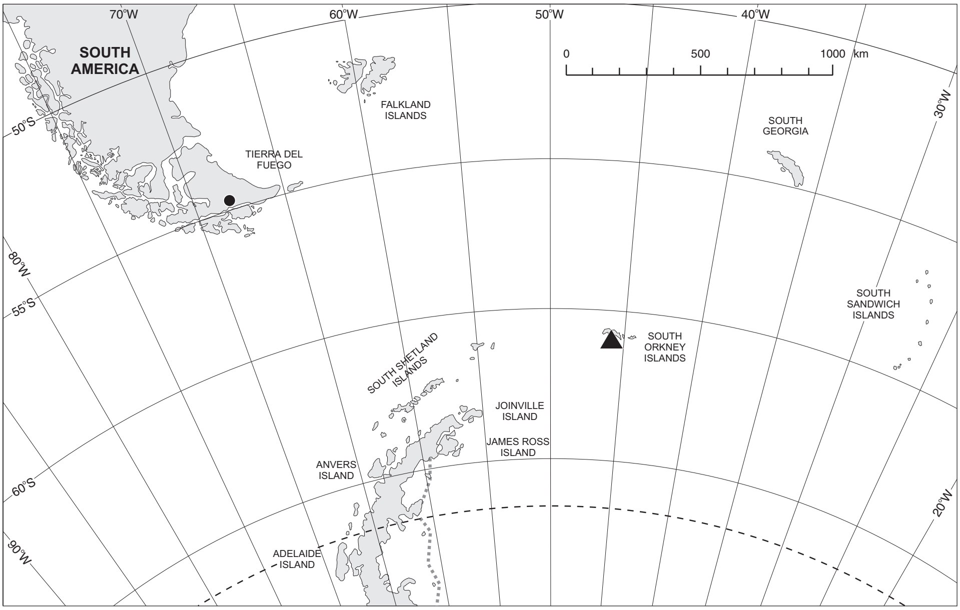

FIGURE 66. Global distribution of *Scapania gamundiae*. The Antarctic locality is indicated by a triangle.

2. *Scapania obcordata* (BERGGR.) S. W. ARNELL FIG. 67

Scapania obcordata (Berggr.) S. W. Arnell *in* S. W. Arnell & Mårtensson, Ark. Bot. Ser. 2, **4**(6): 117. 1959. – *Sarcoscyphus obcordatus* Berggr., K. Svensk. Vet. Akad. Handl. **13**: 96. 1875. – TYPE: [Svalbard] ... auf Beeren Eiland, an den Baien des Eisfjords bis zur Brandewijne Bai und dem Nordkap verbreitet .... [LECTOTYPE (*fide* Schuster, 1974: 268): Nord-Kap, 1868, leg. Berggren – LD (*non* vidi); ISOLECTOTYPE: S!].

Plants small, with *Lophozia*-like habit, usually scattered in mats of other bryophytes, yellowish-brown to brownish. *Stems* 5–10 mm long, soft and fleshy, mostly unbranched, rarely with some terminal or more commonly lateral-intercalary branches, 250–300 µm in diameter; cortex unistratose, ill-defined, composed of thin-walled cells; medullary cells hardly larger than cortical cells, pellucid, leptodermous, slightly collenchymatous, brownish and with copious mycorrhizal infestation at maturity. *Leaves* contiguous to imbricate, obliquely succubously to nearly transversely inserted, conduplicate to more commonly concave-bilobed, with mostly unequal lobes; ventral lobe ovate to broadly ovate, slightly concave, rounded to pointed at the apex, not or only moderately decurrent; dorsal lobe 0.5–0.8 of the size of the ventral lobe, ovate or nearly so, convex, obtuse to apiculate; keel 0.6–0.7 of the length of the ventral lobe, obscurely de-

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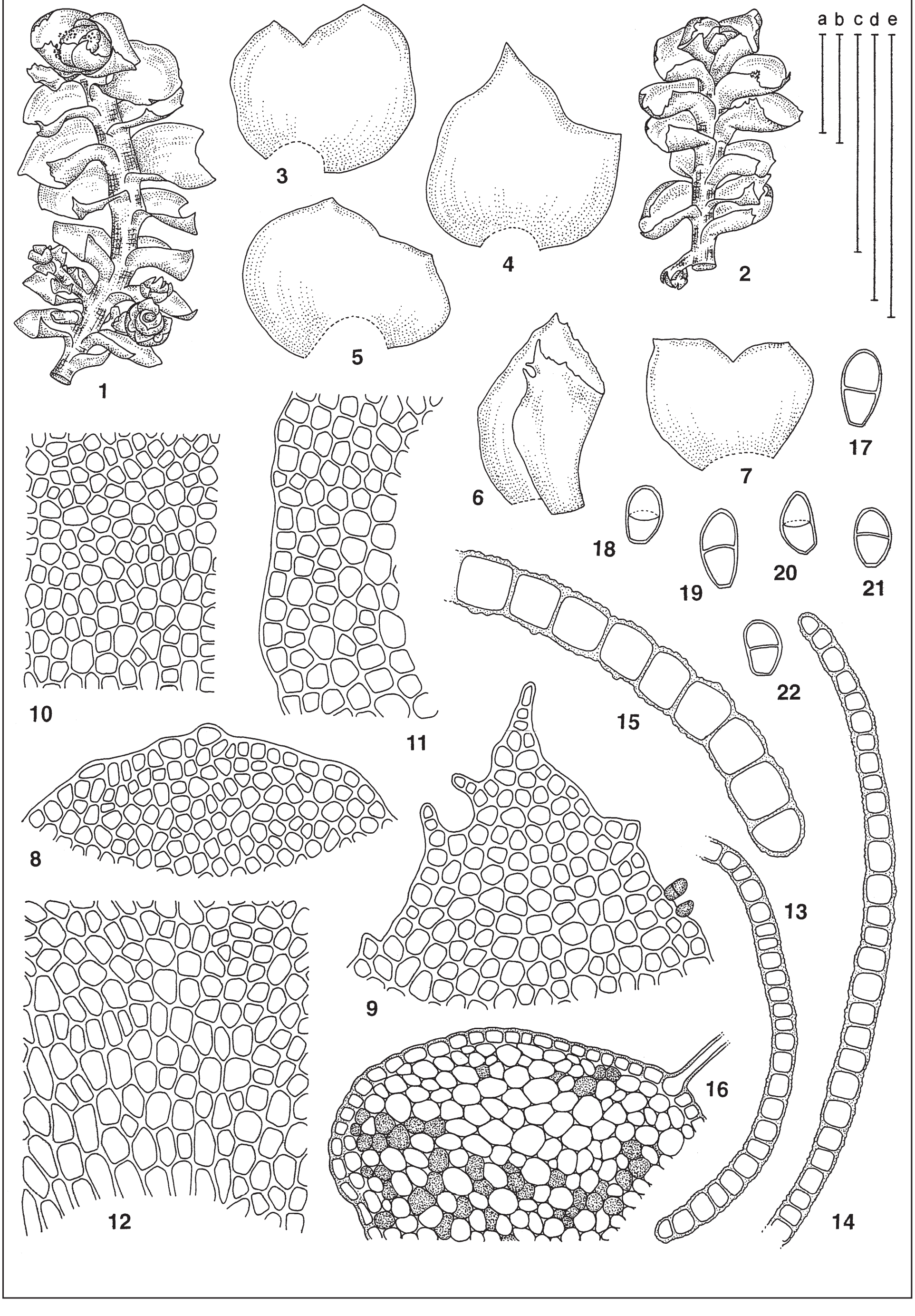
FIGURE 65. *Scapania gamundiae*. **1**. Gemmiparous shoot, ventral view. **2**. Gemmiparous shoot, dorsal view. **3–7**. Leaves, flattened. **8**. Leaf, folded. **9**. Gemmiferous apiculate dorsal lobe. **10–14**. Gemmae. **15–16**. Apices of lobes. **17**. Marginal cells in the upper and median part of ventral lobe. **18**. Mid-leaf cells. **19**. Transverse section of mature stem, showing mycorrhizal infection. (All drawn from *Lewis Smith 682*, AAS.) Scale bars: a – 1 mm (1–2); b – 100 µm (9, 15–19); c – 50 µm (10–14); d – 1 mm (5–8).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veloped and not sharp at any point; leaf margins entire; leaf cells thin-walled with small to large trigones, cell walls brownish; marginal cells 20–25 µm in diameter, median 25–30 µm, basal somewhat elongate to 35(–40) µm; cuticle densely papillose. *Underleaves* absent on Antarctic material. *Gemmae* frequently produced at the apices of the uppermost leaves, frequently broadly ovate, (1–)2-celled, 15–18 × 20–25 µm.

Taxonomic and nomenclatural notes. — *Scapania obcordata* was described by Berggren (1875) as *Sarcoscyphus obcordatus* on the basis of material collected in the Svalbard archipelago and it was transferred to *Scapania* nearly a century later (Arnell & Mårtensson, 1959). The species belongs within subgen. *Jensenia* which accommodates species with weakly keeled or unkeeled leaves, which is a rather anomalous feature in this genus.

Differentiation. — The Antarctic material is very scanty and the two known collections consist of a small number of shoots. The plants are relatively short but otherwise they exhibit all the diagnostic features of the species including a somewhat “lophozioid” rather than “scapanioid” habit, brownish pigmentation and ill-defined keel. On the basis of the cell texture and habit it is readily distinguished from *S. gamundiae*, the only other *Scapania* species known in the austral region. The latter species has smaller, thicker-walled cells and distinct leaf border of 3–4 rows of sometimes tangentially elongate cells, and subequal, mostly squarrose, leaf lobes.

Reproduction in Antarctica. — Fertile plants unknown, but gemmae are frequently produced at the apices of the leaf lobes.

Habitat. — It grows on stony ground in relatively dry places intermingled in mats of *Cephalozia badia* and *Cephaloziella hispidissima*.

World range. — A bipolar species, but predominantly distributed in the High Arctic where it appears to have a widely scattered range. It is known from Alaska (Persson, 1962; Steere & Inoue, 1978), eastern North America from Ellesmere Island south to Great Whale River in Quebec (Persson & Holmen, 1961) and Greenland (Schuster, 1974; Schuster & Damsholt, 1974). In Eurasia it ranges from Iceland to northernmost Finland (see map in Söderström, 1995) and in the Russian Arctic east to the Chukchi Peninsula (Schljakov, 1981) extending as far north as Spitsbergen, with some isolated stations in the North Ural Mountains (Konstantinova *et al*., 1992) and south-eastern Altai (Váňa & Ignatov, 1995) (Fig. 68). In the Southern Hemisphere the species is known only from the Antarctic.

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FIGURE 67. *Scapania obcordata*. **1–2**. Sterile shoots, ventral view. **3–5, 7**. Leaves, flattened. **6**. Leaf, folded. **8**. Apex of blunt dorsal lobe. **9**. Gemmiferous apiculate ventral lobe. **10**. Mid-leaf cells. **11**. Marginal cells in the median part of ventral lobe. **12**. Basal cells in the middle part of leaf. **13–14**. Transverse section through leaves. **15**. Transverse section through leaf showing cuticular papillae. **16**. Transverse section of mature stem, showing mycorrhizal infection. **17–22**. Gemmae. (All from *Lewis Smith 402*, AAS.) Scale bars: a – 1 mm (1–2); b – 100 µm (8–14, 16); c – 1 mm (3–7); d – 100 µm (15); e – 100 µm (17–22).

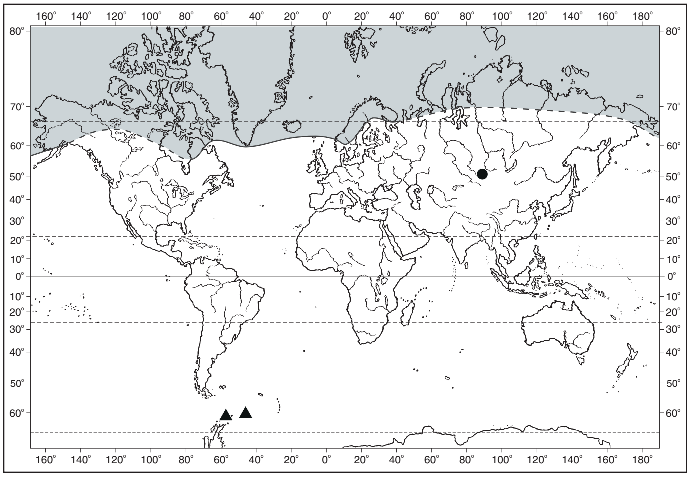


FIGURE 68. Global distribution of *Scapania obcordata*. The Antarctic localities are indicated by triangles.

Distribution in Antarctica. — *Scapania obcordata* is exceedingly rare in the maritime Antarctic and hitherto only two scanty populations have been recorded from Signy Island, in the South Orkney Islands, and King George Island, in the South Shetland Islands (Fig. 69).

Specimens examined. — SOUTH ORKNEY ISLANDS. **SIGNY ISLAND**. Observation Bluff, 50 m, *Lewis Smith 402* (AAS, KRAM).

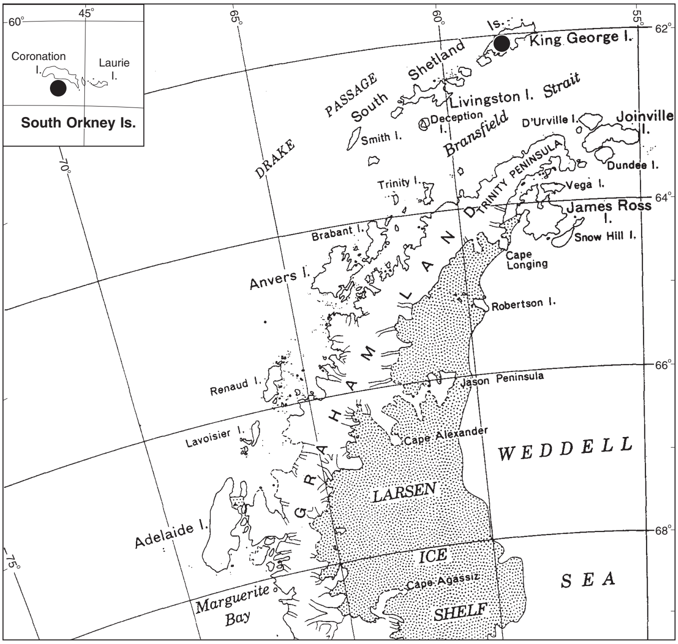


FIGURE 69. Distribution of *Scapania obcordata* in the maritime Antarctic.

SOUTH SHETLAND ISLANDS. **King George Island**. ***Admiralty Bay***: Italia Valley, 100 m, *Ochyra 88A/80 & 91A/80* (KRAM, PRC).

Literature records. — SOUTH SHETLAND ISLANDS: King George Island (Bonner & Lewis Smith, 1985: 168; Ochyra & Váňa, 1989*a*: 205; 1989*b*: 218; Myrcha *et al.*, 1991: 163).

Family **IX. GEOCALYCACEAE** H. KLINGGR.

Geocalycaceae H. Klinggr., Höh. Crypt. Preuss.: 34. 1858 ["Geocalycinae"]. – TYPE: *Geocalyx* Nees.

Plants very small to large and robust, anisophyllous or rarely subisophyllous, light to dark green, yellowish-green or brownish-green, rarely developing secondary pigmentation, yellow- or red-brown, brown to blackish. *Stems* soft-textured, simple or more commonly branched; branching very variable: terminal (*Frullania*-type), lateral-intercalary (*Plagiochila*-type, in *Evansianthus* also *Andrewsianthus*-type) or ventral-intercalary (*Bazzania*-type); stolons occasionally present; flagellae absent; cortical cells not or hardly differentiated, mostly thin-walled (excl. *Pachyglossa*); mycorrhizae absent. *Rhizoids* dispersed on the ventral side of stem, mostly clustered at bases of the underleaves. *Leaves* succubously to nearly longitudinally inserted, alternate to subopposite, sometimes connate, mostly bilobed, rarely unlobed or trilobed, with entire, toothed or crenulate margins; leaf cells very variable, mostly thin- or slightly thick-walled, with no or small trigones. *Underleaves* mostly much smaller than lateral leaves, bifid to unlobed, mostly with lateral teeth, sometimes connate with one or rarely both leaves. *Asexual reproduction* occasional, mostly by few-celled gemmae, exceptionally by caducous leaf apices. *Dioecious* or *monoecious* (mostly autoecious, but also paroecious). *Androecia* terminal, becoming intercalary, mostly spicate; male bracts similar to leaves, saccate, with 1–2(–4) antheridia per bract; antheridial stalk 1–2(–4) seriate; bracteoles without antheridia. *Gynoecia* on the main stem or lateral-intercalary to ventral-intercalary branches; female bracts large to reduced. Perianth present, strongly trigonous, with the third keel antical, occasionally laterally compressed, in some genera reduced. *Seta* of many cell rows to reduced to 3 cell rows (16–18 + 8–12 + 4) or two cell rows (8–9 + 4). *Capsule* ovoid to cylindrical; capsule wall of 3–6(–8) layers; outer layer with nodular and sometimes with semiannular thickenings, inner layer with semiannular thickenings. *Spores* globose, smooth to papilose; spore/elater width ratio mostly 1–2 : 1.

The Geocalycaceae are a polymorphous, isolated group with no obvious relationships to other families except for the Brevianthaceae. It has been variously interpreted, but now a rather broad familial concept is accepted to include in it the family Lophocoleaceae (Schuster, 1980*a*; Grolle, 1983*a*). Two distinct complexes are recognised as separate subfamilies: Geocalycoideae comprising four genera with a biseriate antheridial stalk, and Lophocoleoideae comprising 17 genera with a uniseriate antheridial stalk. These have been overviewed by Engel and Schuster (1984). Sometimes a third subfamily, Leptoscyphoideae, is segregated from the latter (Schuster, 1980*a*; Schuster & Engel, 1982).

The family has a worldwide distribution but it shows greater specific and generic diversity in the cool and temperate sectors of the Southern Hemisphere and in the tropics, with several genera endemic to the cool antipodal regions. It is the family with the most species represented in the Antarctic, consisting of six belonging within four genera which are separated in the following key.

KEY TO THE ANTARCTIC GENERA OF THE GEOCALYCACEAE

1. Plants anisophyllous. Leaves always unistratose (regional taxa) and bilobed, underleaves bifid, with marginal additional teeth 2
1. Plants subisophyllous or anisophyllous; leaves, at least in the basal part (in *Pachyglossa spegazziniana*) bi- or polystratose, mostly unlobed or only some leaves retuse to slightly bilobed (in this case plants subisophyllous and underleaves mostly unlobed) 3

2. Leaves concave, widely ovate; underleaves often obliquely inserted . . . . **1. *Clasmatocolea***
2. Leaves convex, rectangular to narrowly ovate; underleaves constantly transversely oriented . . . . **3. *Lophocolea***

3. Anisophyllous plants with small underleaves; branching of the *Andrewsianthus*-type present; leaves orbicular to reniform, always unlobed . . . . **2. *Evansianthus***
3. Subisophyllous to anisophyllous plants with large underleaves; branching of the *Andrewsianthus*-type absent; leaves ovate to lingulate, if broadly ovate to suborbicular then at least some leaves incised or slightly bilobed . . . . **4. *Pachyglossa***

1. CLASMATOCOLEA SPRUCE

Clasmatocolea Spruce, Trans. Proc. Bot. Soc. Edinburgh **15**: 440. 1885. – LECTOTYPE: *Clasmatocolea heterostipa* Spruce (*fide* Grolle, 1956: 289–290).

Plants small, brownish-green to brownish, in loose or dense interwoven pure mats or tufts or mixed with other bryophytes. *Stems* prostrate to suberect, mostly lateral-intercalary to ventral-intercalary branched, without stolons; cortex hardly differentiated from medullary cells, of 1–3 cell rows. *Rhizoids* colourless or crimson, arising near underleaf base or sometimes from ventral leaf base. *Leaves* unistratose or rarely with 2–4-stratose margins forming a fleshy border or with 2–4-stratose median-basal area, succubously oriented, conchiform concave, undivided or bilobed, rarely trilobed or with accessory lobes; margins mostly entire, sometimes with teeth or laciniae; leaf cells thin- to moderately thick-walled, with large or small trigones; cuticle smooth to roughened or coarsely papillose or verrucose. *Underleaves* small, plane or convex, undivided, retuse to bilobed, with the apical teeth terminating in a slime papilla. *Gemmae* absent. *Dioecious*. *Androecia* terminal, becoming intercalary on leading shoots or short branches; male bracts saccate, with 1(–2) antheridia per bract. *Gynoecia* terminal on main axes or abbreviated branches, female bracts progresively larger towards the perianth. *Perianth* inflated, weakly to strongly trigonous or terete, particularly towards the base, with a wide, exceptionally contracted, trilobed mouth. *Seta* in transverse section composed of undifferentiated cells. *Capsule* wall 3–6-stratose. *Spores* light brown-brown, finely papillose; elaters bispiral; spore/elater width ratio 1.0–2.8 : 1.

Clasmatocolea has been misunderstood since its description by Spruce (1885) and, until the 1960s, it has been variously interpreted. In his first assessment of the genus Grolle (1956) considered *Clasmatocolea* as a monotype consisting of only *C. heterostipa*, but later he expanded the concept of this genus and placed 18 species in it (Grolle, 1960*b*). Engel (1980) published a thorough monograph of *Clasmatocolea* and recognised 20 species in this genus divided into six subgenera, and later Engel (1990*b*, 1991) added one more species from Australia and Tasmania. *Clasmatoclea* is antipodal in distribution and its species are largely restricted to cool south-temperate and subantarctic regions in the Southern Hemisphere, with a single species, *C. tjiwideiensis*, which is restricted to mountainous areas in the Malesian region. Only one species, *C. rigens* of subgen. *Protoclasmatocolea* is known to occur in the Antarctic.

1. ***Clasmatocolea rigens*** (Hook. f. & Taylor) J. J. Engel Fig. 70

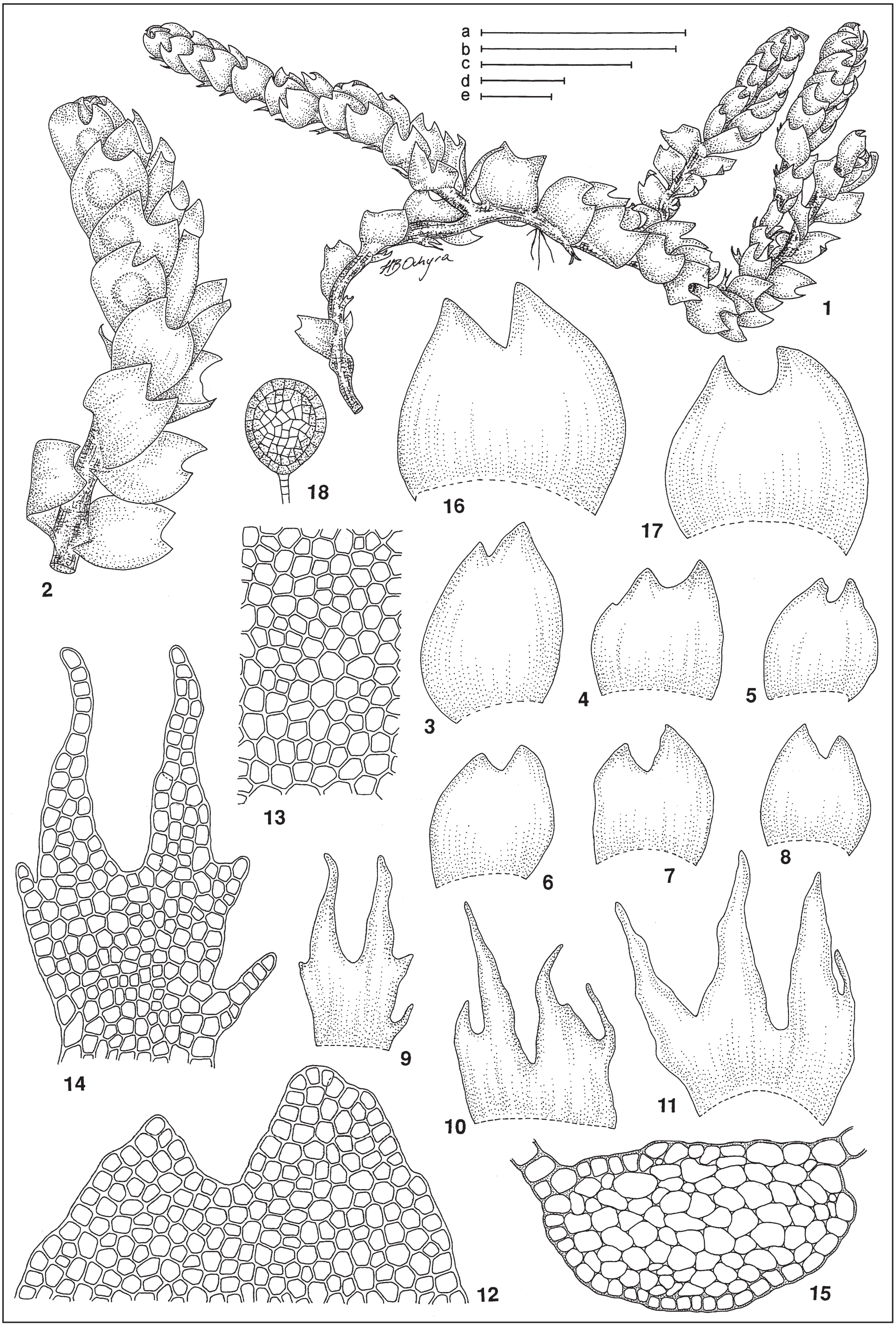
Clasmatocolea rigens (Hook. f. & Taylor) J. J. Engel, J. Hattori Bot. Lab. **36**: 156. 1973. – *Jungermannia rigens* Hook. f. & Taylor, London J. Bot. **3**: 461. 1844. – *Cephalozia rigens* (Hook. f. & Taylor) Trevis., Mem. R. Ist. Lombard. Sci. Lett. Ser. 3, **4**: 417. 1877. – *Lophocolea rigens* (Hook. f. & Taylor) A. Evans, Bull. Torrey Bot. Cl. **25**: 423. 1898. – Type: Falkland Islands, Hooker [Holotype: “Jungermannia rigens Tayl mss Falkland Islands J. D. Hooker 1843” – FH-Taylor!; isotype: BM-Hook!].

Lophocolea koeppensis Gottsche *in* Neumayer, Deutsch. Exp. Int. Polarforsch. **2**: 453, *p. 2, f. 4–9*. 1890. – *Clasmatocolea koeppensis* (Gottsche) Grolle, Rev. Bryol. Lichénol. **29**: 72. 1960. – Type: Dr Will Nr. 35. Süd-Georgien. Köppenberg, 10. Februar 1883 [Lectotype (*fide* Grolle, 1972*a*: 86): M (*non vidi*)].

Plants small, rather fragile, in dense mats or scattered amongst mosses, pale green to yellowish-brown, somewhat glossy when dry. *Stems* prostrate, terminally or lateral-intercalary, rarely ventral-intercalary branched, with branches relatively short, to 2 mm, in transverse section 6–8 cells high; cortex unistratose composed of slightly smaller or the same size as medullary cells, with thin to firm walls; medullary cells larger, thin-waller, with small trigones. *Rhizoids* clustered at underleaf bases. *Leaves* erect, loosely imbricate, succubously inserted, concave, ovate to widely ovate, usually longer than wide but widely ovate leaves commonly wider than long, bifid to 0.1–0.3 of their length; lobes triangular, apiculate to subapiculate, incurved, sinus rounded to lunate; margins mostly entire; leaf cells thin-walled, with small trigones, 15–35 × 18–38 µm µm; cuticle smooth or roughened and appearing finely granular. *Underleaves* slightly wider than stem, obliquely inserted, bilobed to (0.5–)0.7–0.9 their length, rarely atypically trilobed; segments lanceolate-subulate, apiculate, terminating with a slime papilla; margins 1–2(–3)-dentate-laciniate-subulate, also ending with a slime papilla. *Dioecious*. Only male plants seen. *Androecia* terminal, becoming intercalary, on main axis; male bracts strongly saccate, monandrous; antheridia with a uniseriate stalk. *Remainder* unknown in Antarctic material.

Taxonomic and nomenclatural notes. — *Clasmatocolea rigens* was originally described from the Falkland Islands by Hooker and Taylor (1844) as *Jungermannia rigens*. The type material comprises very small plants resembling *Cephalozia* and this prompted Trevisan (1877) to transfer this species to that genus. Evans (1898) then transferred it to *Lophocolea*, thus correctly indicating its familial affinity, and finally Engel (1973*b*) placed it in the correct genus. In the subantarctic region the species was long known as *C. koeppensis* and, in fact, under this name it was first reported from the Antarctic (Grolle, 1972*a*). This species, described originally from South Georgia as *Lophocolea koeppensis*, was shown to be conspecific with *C. rigens* by Engel (1973*b*).

Differentiation. — *Clasmatocolea rigens* is a distinct species which should not be confused with other liverwort taxa in Antarctica. Its concave, widely ovate and bifid leaves combined with small underleaves which are mostly obliquely, not transversely, inserted and bifid nearly to the base are characteristic features of this otherwise distinct species.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Reproduction in Antarctica. — Fertile plants unknown, but male plants have been found.

Habitat. — On ash, gravel and scoria around fumaroles moistened and probably warmed by steam.

World range. — A South American temperate species, occurring in the *Nothofagus* zone along the western coast of the continent from Central Chile to Tierra del Fuego, and including the Falkland Islands and South Georgia (Engel, 1980) (Fig. 71).

Distribution in Antarctica. — Apparently very rare, known only from two small islands in the South Sandwich Islands archipelago from sea level to 135 m (Fig. 71). Schuster (1996*b*) mentioned *Clasmatocolea rigens* (as *C. koeppensis*) from King George Island in the South Shetlands on the basis of a specimen (*Ochyra 88/80*) from the Admiralty Bay area, which he described as also containing an admixture of *Herzogobryum teres* and *Pachyglossa dissitifolia*. Our examinarion of this specimen, however, revealed these two associates, together with a few shoots of *Scapania obcordata* with fine gemmae, but no *Clasmatocolea* was seen. Thus, the occurrence of this species in the South Shetland Islands cannot be confirmed.

Specimens examined. — SOUTH SANDWICH ISLANDS. **Saunders Island**. North end, *ca* 15 m, *Holdgate 434A* (AAS, KRAM). **Bellingshausen Island**. Southern slopes, 25 m, *Holdgate 811C & 816C* (AAS, KRAM) and *ca* 85 m, *Holdgate 419B, 420A & 421B* (AAS, KRAM); east end of rim within the crater, *ca* 65 m, *Holdgate 825B* (AAS, KRAM); within main crater on west side, *ca* 135 m, *Holdgate 430A, 431A & 479* (AAS, KRAM); southern coast at mouth of nearly dead fumaroles, *Convey 75D* (AAS, KRAM).

Literature records. — SOUTH SANDWICH ISLANDS: without indication of the island (Lewis Smith, 1993: 322 as *Clasmatocolea koeppensis*); Saunders and Bellingshausen Islands (Grolle, 1972*a*: 84; Longton & Holdgate, 1979: 10 both as *C. koeppensis*; Engel, 1980: 49; Ochyra & Váňa, 1989*b*: 218). SOUTH SHETLAND ISLANDS: King George Island (Schuster, 1996*b*: 35).

2. EVANSIANTHUS R. M. SCHUST. & J. J. ENGEL

Evansianthus R. M. Schust. & J. J. Engel, Bryologist **76**: 516, *f. 1–9*. 1973. – HOLOTYPE: *Evansianthus georgiensis* (Gottsche) R. M. Schust. & J. J. Engel (*Lophocolea georgiensis* Gottsche).

Plants small, in dense tufts or patches, green or light brown, becoming blackish on drying. *Stems* prostrate, intricately dorsal-intercalary branched (*Andrewsianthus*-type), sometimes with microphyllous flagellae and subterranean rhizome-like extensions of main axes; cortex undiff-

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FIGURE 70. *Clasmatocolea rigens*. **1**. Sterile shoot, dorso-lateral view. **2**. Portion of main shoot, lateral view. **3–8**. Leaves. **9–11**. Underleaves. **12**. Cells at leaf lobes. **13**. Mid-leaf cells. **14**. Cells of amphigastrium. **15**. Transverse section of stem. **16–17**. Male bracts. **18**. Antheridium. (All from *Holdgate 431A*, AAS.) Scale bars: a – 0.5 mm (9–11) and 1 mm (3–8, 16–17); b – 0.5 mm (18); c – 1 mm (2); d – 100 µm (12–15); e – 1 mm (1).

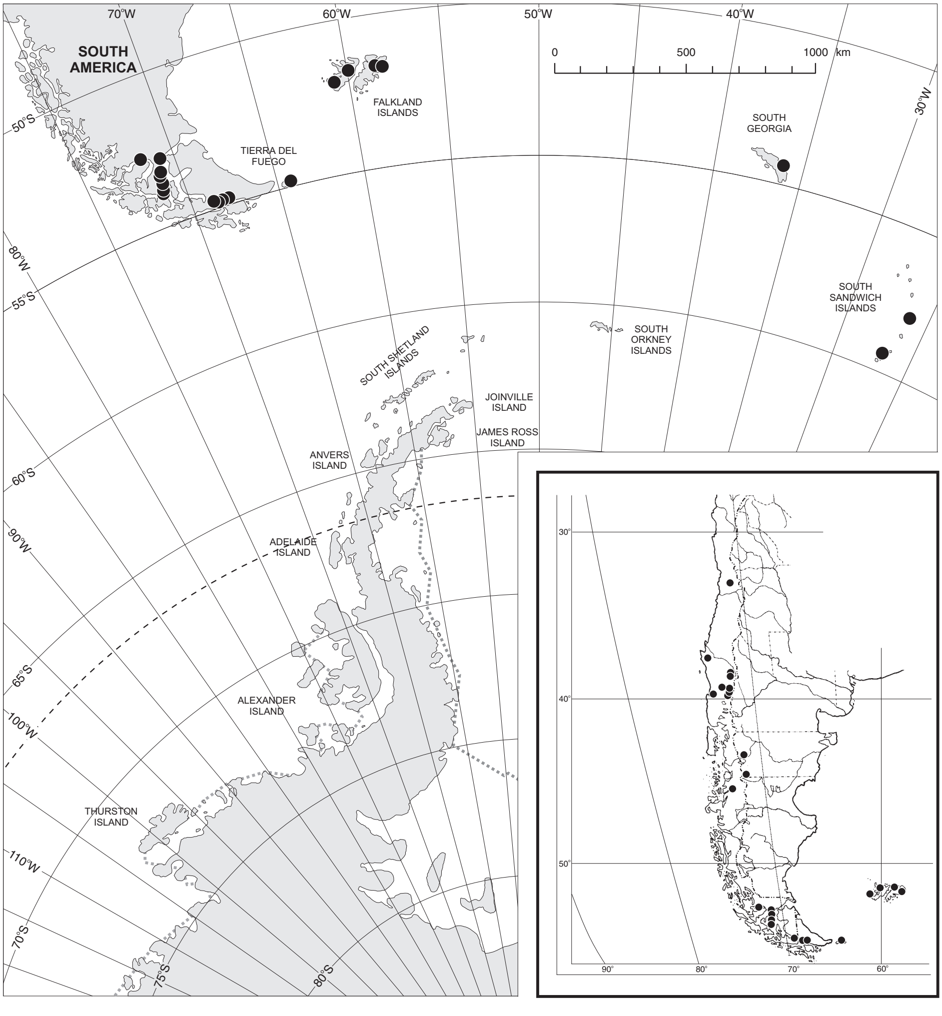


FIGURE 71. Distribution of *Clasmatocolea rigens* in the Antarctic and Fuegian region. Inset: distribution in South America.

erentiated. *Rhizoids* frequent, colourless, arising at underleaf bases or at base of scale-like leaves on stolon-like branches or rhizomatous extensions of main axis. *Leaves* imbricate, vertical, alternate, erecto-patent to suberect, orbicular to reniform, concave, 2–5-stratose in median and basal portions, unistratose in peripheral portion, very broadly rounded to rounded-truncate at the apex, unlobed or occasionally broadly retuse to emarginate; margins entire, unistratose; leaf cells small, thin-walled, minutely collenchymatous; cuticle smooth. *Underleaves* small, appressed to spreading, ovate or oblong to ovate-triangular, shallowly bifid to 0.1–0.3 the length, bidentate or subentire; lobes ending with a slime papilla. *Gemmae* absent. *Autoecious*. *Androecia* terminal or intercalary on short to elongate branches; male bracts small, ovate to orbicular, unlobed or with a single lobe, monandrous or occasionally with 2 antheridia; antheridial stalk biseriate. *Gynoecia* on abbreviated branches; female bracts similar to leaves, polystratose in median and basal parts, erect-appressed, vertical, entire-margined; bracteoles free from bracts, ovate-triangular to bifid. *Perianth* laterally compressed, deeply bilobate with a third, ± retuse, ventral lobe, wide at mouth; mouth entire or bluntly denticulate to lobulate. *Seta* 10–11 cells wide. *Capsule* subspherical to ellipsoid, with 4–6-stratose wall. *Spores* globose, red-brown, verrucose; elaters bispiral, red-brown; spore/elater width ratio 2–2.5 : 1.

A monotypic genus established by Schuster and Engel (1973) to accommodate the South Georgian and southern South American *Lophocolea georgiensis* Gottsche. This taxon comprises anisophyllous plants with small underleaves and it is characterised by the presence of the dorsal-intercalary, *Andrewsianthus*-type branching which is unknown in any other taxa of the Geocalycaceae. Additionally, it is diagnosed by its vertical, unlobed, orbicular to reniform, multistratose, deeply concave leaves.

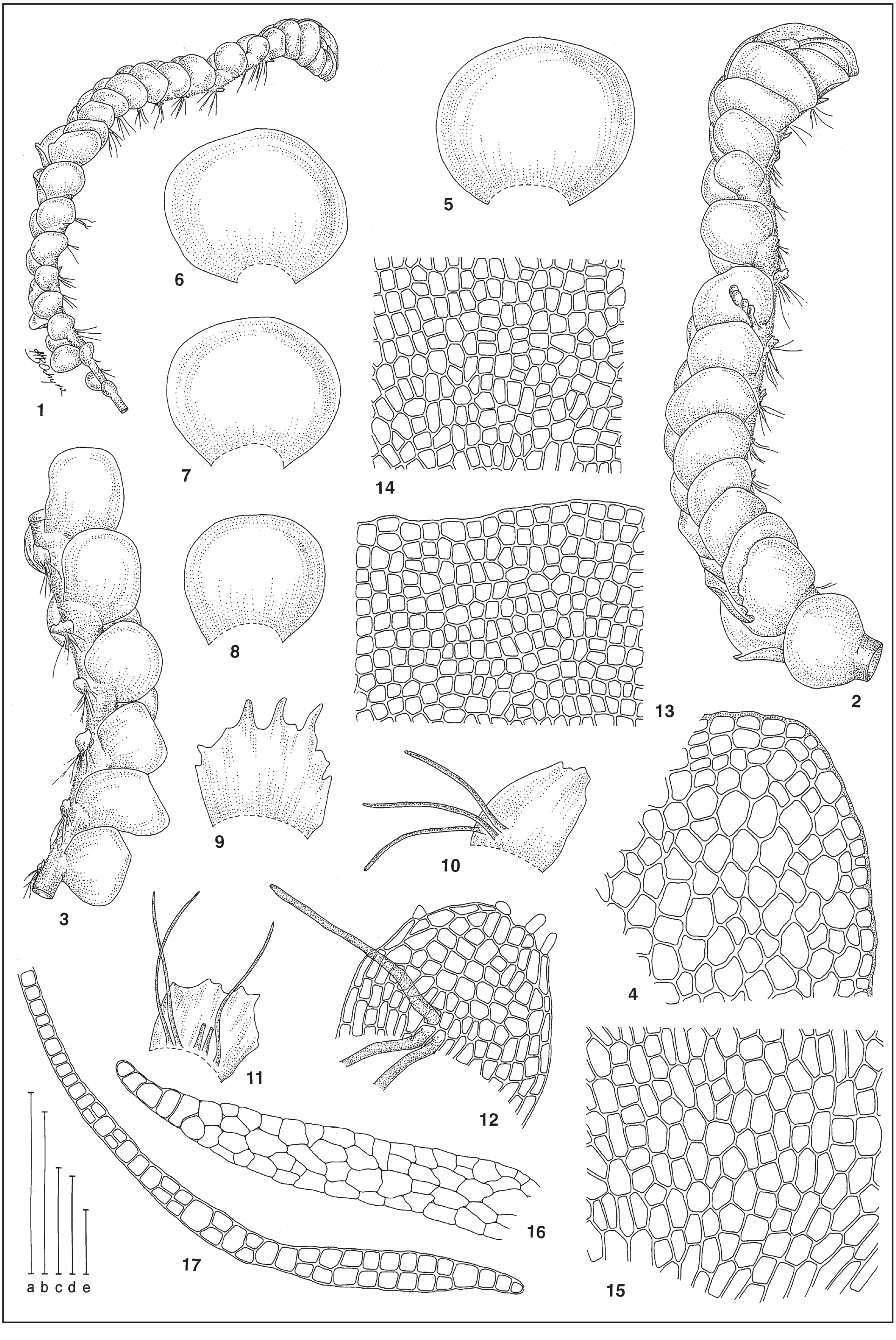
1. ***Evansianthus georgiensis*** (GOTTSCHE) R. M. SCHUST. & J. J. ENGEL FIG. 72

Evansianthus georgiensis (Gottsche) R. M. Schust. & J. J. Engel, Bryologist **76**: 518, *f. 1–9*. 1973. – *Lophocolea georgiensis* Gottsche *in* Neumayer, Deutsch. Exp. Int. Polarforsch. **2**: 453. 1890. – *Clasmatocolea georgiensis* (Gottsche) Grolle, Brit. Antarct. Surv. Bull. **28**: 86. 1972 [*Clasmatocolea georgiensis* (Gottsche) R. M. Schust., Antarct. J. U. S. **4**(4): 103. 1969, *comb. inval. basion. non citat.*]. – TYPE: Dr. Will Nr. 11. Süd-Georgien. In Felsspalten im Hintergrund des Thales rechts vom Südwestgletscher. Südgletscher, 10. Mai 1883 [LECTOTYPE (*fide* Schuster & Engel, 1973: 518): "№. 11 Nova Georgiensis Orig. Gottsche. In Felsspaltenm hinteren Grund des Thales rechts vom Südgletcher Südgeorgien 10/V 83 W.[ill]" – M!].

Plants small, with leafy shoots 5–12 mm long, fleshy and rather brittle in texture. *Stems* prostrate, in transverse section 9–15 cells high; cortical cells in 1–2(–3) layers thin- to slightly firm-walled, 11–24 µm in diameter; medullary cells thin-walled, larger, 24–38 µm in diameter. *Leaves* imbricate, vertical, alternate, erecto-patent to suberect, broadly orbicular to reniform, strongly concave, 1.7–2.4 mm wide, 1.1–1.2 mm long; leaf cells small, thin-walled, 15–30 × 20–43 µm in mid-leaf, becoming more leptodermous and larger near base, 18–36 × 30–56 µm. *Underleaves* small, 0.25–0.35 mm long, 0.30–0.35 mm wide. *Spores* 16–22 µm in diameter; elaters 11 µm wide.

Taxonomic and nomenclatural notes. — *Evansianthus georgiensis* was originally described from a single collection from South Georgia as *Lophocolea georgiensis* (Gottsche, 1890), and later Grolle (1972*a*) and Engel (1973*b*) transferred it to *Clasmatocolea*. However, Schuster and Engel (1973) found that it is a discordant element in this genus and created the monotypic genus *Evansianthus* to accommodate it.

Differentiation. — In the Antarctic *Evansianthus georgiensis* could be mistaken for *Hygrolembidium ventrosum* with which it shares a similarly anisophyllous habit and multistratose leaves. The essential difference between these taxa is in the type of branching, dorsal-intercalary in *Evansianthus* compared with ventral-intercalary in *Hygrolembidium ventrosum*. In addition, the former has broadly orbicular to reniform, entire-margined leaves, bifid or bidentate underleaves and compressed perianth, in contrast to irregularly ovate leaves with repand margins, underleaves crenate at the top and cylindrical perianth in *H. ventrosum*.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Reproduction in Antarctica. — No information.

Habitat. — No information on habitat in Antarctica is available, but Schuster (1982) stated that *Evansianthus georgiensis* was collected “essentially at sea level in a region that was deglaciated in relatively recent times”. This implies that it is a pioneer liverwort growing on bare soil.

World range. — *Evansianthus georgiensis* is strictly subantarctic in distribution (Fig. 73). It is frequent on South Georgia from where it was originally described (Gottsche, 1890; Grolle, 1972*a*), the Falkland Islands (Engel, 1990*a*) and Tierra del Fuego, Brunswick Peninsula and in Magellan Strait islands (Schuster & Engel, 1973; Engel, 1978), but at the more northerly stations it occurs at high elevations. Therefore, the range of this taxon must be interpreted as subantarctic. Schuster and Engel (1973) did not cite any material from Antarctica, although

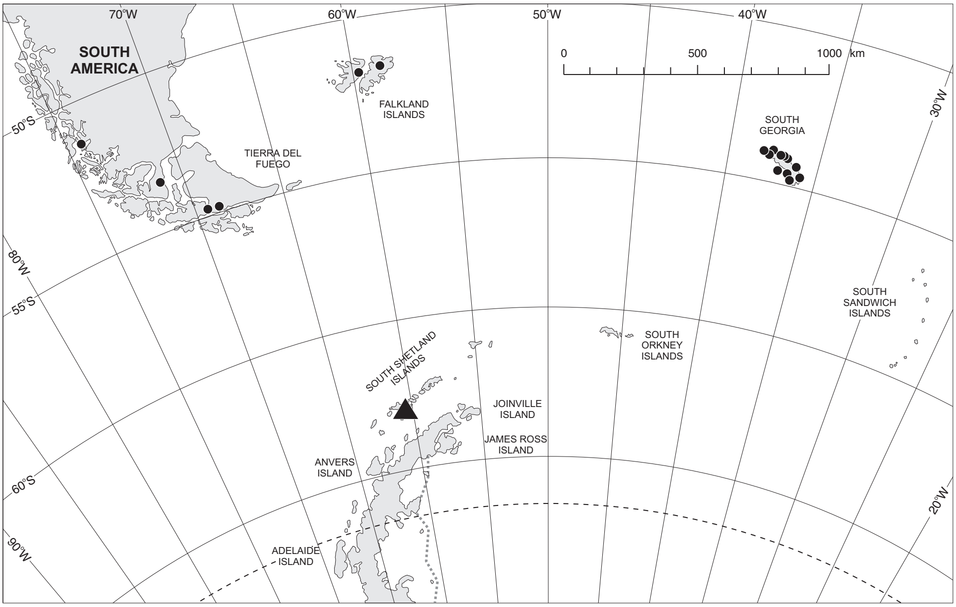

FIGURE 73. Global distribution of *Evansianthus georgiensis*. The Antarctic locality is indicated by a triangle.

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FIGURE 72. *Evansianthus georgiensis*. **1**. Sterile plant. **2–3**. Shoots, partly in lateral, partly in postical aspect. **4**. Transverse section of stem. **5–8**. Leaves. **9**. Underleaf. **10–11**. Underleaves showing rhizoids. **12**. Areolation of underleaf and rhizoids. **13**. Cells of leaf margin. **14**. Mid-leaf cells. **15**. Cells at leaf base. **16**. Transverse section of leaf near base. **17**. Transverse section of leaf near the middle. (All from *Will 11*, type of *Lophocolea georgiensis*, M). Scale bars: a – 0.5 mm (9–11; b – 5 mm (1) and 2 mm (3); c – 1 mm (5–8); d – 100 µm (4); e – 100 µm (12–17) and 1 mm (2).

R. M. Schuster allegedly collected it on 25 January 1969 when he visited Livingston Island (see Robinson, 1972 for details of his collecting sites in the Antarctic). Schuster (1969*a*) originally cited *Clasmatocolea georgiensis* (=*Evansianthus georgiensis*) from the Antarctic Peninsula region, but later he (Schuster, 1982 and personal communication) admitted that the material was collected on Livingston Island in the South Shetland Islands

Distribution in Antarctica. — *Evansianthus georgiensis* has only once been collected. This was near sea level at the east side of False Bay on Hurd Peninsula, Livingston Island at lat. 62°43'S (Fig. 73).

Specimens examined. — No material from Antarctica seen. The species was described and illustrated on the basis of the South Georgian type material preserved at M.

Literature records. — SOUTH SHETLAND ISLANDS: Livingston Island (Schuster, 1969*a*: 103; 1980: 175; 1982: 17; Ochyra & Váňa, 1989*b*: 218).

3. LOPHOCOLEA (DUMORT.) DUMORT.

Lophocolea (Dumort.) Dumort., Recueil Observ. Jung.: 17. 1835. – *Jungermannia* L. sect. *Lophocolea* Dumort., Sylloge Jung. Eur. Indig.: 59. 1831. – LECTOTYPE: *Lophocolea bidentata* (L.) Dumort. (*Jungermannia bidentata* L.) (*fide* Hamlin, 1972: 333).

Plants very small to medium-sized or sometimes large, in dense or loose flat patches or mats, varying from very pale green or yellowish-green to bright, greyish or dark green, sometimes becoming brownish-green with age, translucent, strongly fragrant when fresh, mostly anisophyllous. *Stems* prostrate to ascending, freely branched with terminal, lateral-intercalary to ventral-intercalary branches, cortex in 1–2 rows hardly differentiated into somewhat smaller cells or undifferentiated. *Rhizoids* usually freely produced, mostly confined to or near underleaf insertion. *Leaves* succubous, obliquely to nearly longitudinally inserted, alternate to subopposite, subrectangular, subquadrate, suborbicular to ovate, plane to weakly or strongly convex, mostly bilobed, but also unlobed or trilobed; lobes divergent to connivent, triangular or ovate-triangular to subulate; sinus narrowly rounded or subacute to rectangulate or lunate; leaf cells subquadrate to hexagonal, thin- or slightly thick-walled, mostly without trigones or with small trigones; cuticle smooth. *Underleaves* deeply bifid, with one to several teeth on lateral margins, free or connate with one to both leaves. *Gemmae* produced on leaf margins in few species, 1–few-celled, often polymorphous. *Dioecious*, rarely *monoecious*. *Male inflorescence* spiciform becoming intercalary, on the main stem or short ventral-intercalary branch; male bracts saccate, edentate or less often dentate, monandrous; antheridial stalk 1(–2)-seriate. *Gynoecia* terminal on the main axis or branch; female bracts and subinvolucral leaves bilobed or less often retuse, similar to leaves but larger; bracteoles free or occasionally connate with a bract, larger than underleaves. *Perianth* sharply trigonous, keels mostly winged or toothed, with 3-lobed mouth. *Capsule* mostly ovoid, with 4–6-stratose wall; outer wall with nodulose and inner wall with semiannulate thickenings. *Spores* smooth, 8–22 µm in diameter.

Lophocolea is one of the largest of all liverwort genera consisting of about 300 described species, many of which probably do not deserve taxonomic recognition. Most occur in the tropics and in the Southern Hemisphere. Engel and Schuster (1984) considered *Lophocolea* to be congeneric with *Chiloscyphus*, and as a result 223

Lophocolea species were given names under *Chiloscyphus*. This concept was criticised by Grolle (1995) because, except for numerous nomenclatural changes, it has not contributed significantly to the taxonomy of this otherwise difficult complex. In the present treatment *Lophocolea* is accepted in its traditional sense as a separate genus. The genus was monographed in South America by Fulford (1976) where it is represented by about 40 species. One of them, *L. lenta*, extends to Antarctica.

1. ***Lophocolea lenta*** (Hook. f. & Taylor) Gottsche, Lindenb. & Nees Fig. 74

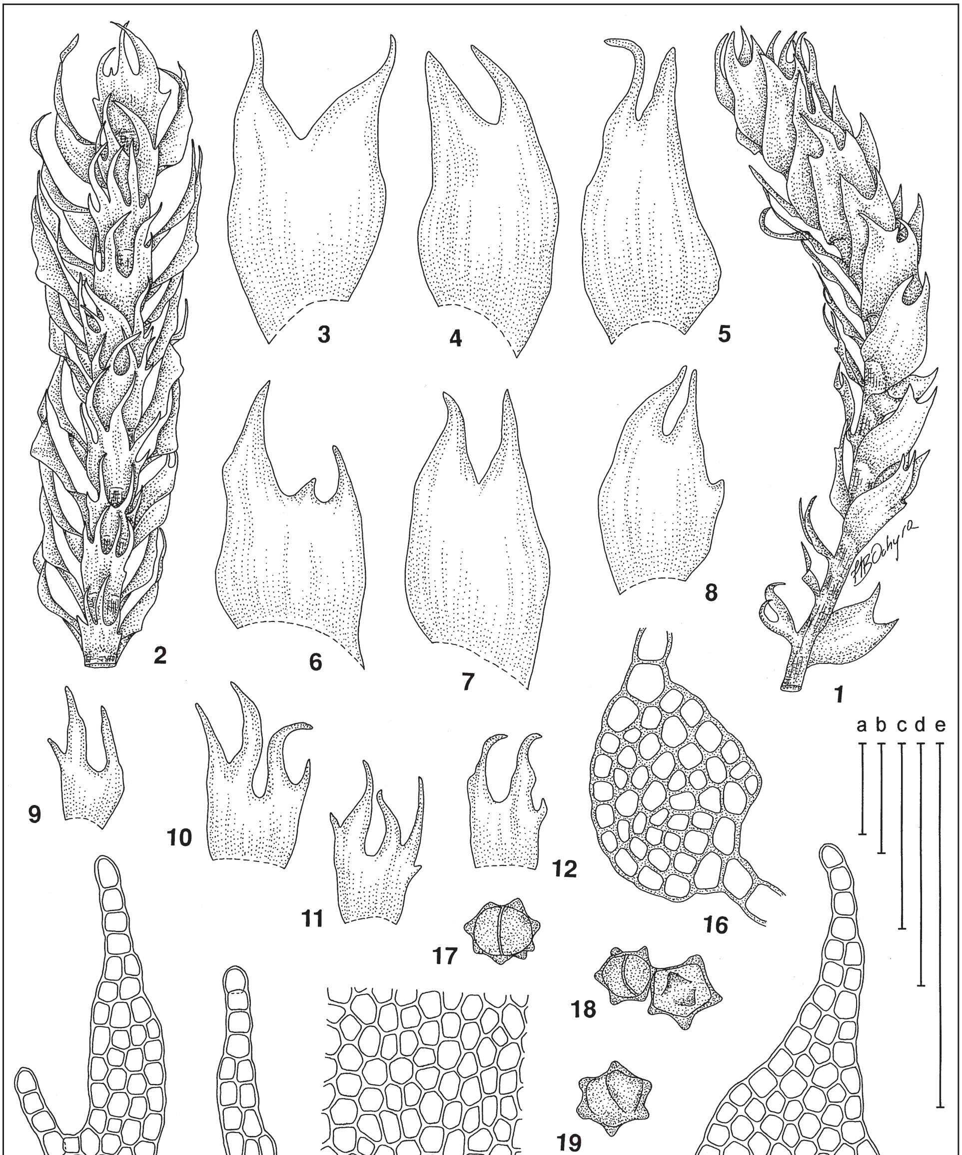
Lophocolea lenta (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat.: 162. 1845. – *Jungermannia lenta* Hook. f. & Taylor, London J. Bot. **3**: 379. 1844. – *Chiloscyphus lentus* (Hook. f. & Taylor) J. J. Engel & R. M. Schust., Nova Hedwigia **39**: 418. 1984. – Type: Lord Auckland's group [Holotype: "Jungermannia lenta Tayl. mss (Lophocolea) Lord Auckland's Group Nov. 1840 Joseph D. Hooker" – FH-taylor! isotype: BM-hook!].

Jungermannia secundifolia Hook. f. & Taylor, London J. Bot. **3**: 471. 1844. – *Lophocolea secundifolia* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat.: 693. 1847. – Type: Falkland Islands [Lectotype (*fide* Engel, 1978: 190): "Jungermannia secundifolia Tayl. mss (Lophocolea) Falkland Islands J. D Hooker 1843" – FH-taylor!; isotype: BM-hook!]. First synonymised by Mitten (1855).

Plants small, in dense patches or mats, or intermixed amongst other bryophytes, 1–3 cm long with shoots to 1.5 mm wide, light-greenish or yellowish- to whitish-green. *Stems* prostrate or ascending, mostly simple, rarely with lateral-intercalary branches, stiff and rigid, in transverse section 8–10 cells high; cortical cells undifferentiated from medullary cells, large, thick-walled. *Rhizoids* in clusters, mostly restricted to underleaf bases. *Leaves* obliquely inserted, subopposite, convex or plane, contiguous, widely erect-spreading to erecto-connivent, narrowly ovate-truncate to subrectangular, 0.5–1.0 × 0.4–0.6 mm, bifid to 0.3–0.5 their length; lobes triangular to subulate, divergent, straight, ending in a few-celled uniseriate tip; sinus acute, deep; leaf cells with slightly thickened walls, without trigones, 22–28 µm in diameter; cuticle verruculose. *Underleaves* relatively large to small, usually larger than stem, bifid nearly to the middle, with one or two lateral teeth. *Gemmae* occasionally present, 2-celled, stellate. Gynoecia terminal on the main axis; female bracts and subinvolucral leaves bilobed or less often retuse, similar to leaves but larger; bracteoles free or occasionally connate with a bract, larger than underleaves. *Perianth* sharply trigonous, long exserted, lobes with incised margins. *Sporophytes* unknown in the Antarctic.

Taxonomic and nomenclatural notes. — *Lophocolea lenta* was described as *Jungermannia lenta* by Hooker and Taylor (1844) from material collected on the Auckland Islands by the first author during his Antarctic voyage of 1839–1843. It was transferred to *Lophocolea* by Gottsche *et al*. (1845), and remained as a member of this genus until Engel and Schuster (1984) transferred it to *Chiloscyphus*. The Antarctic plants were initially recognised as *Lophocolea secundifolia*. However, this species has a similar history to *L. lenta* and was described by Hooker and Taylor (1844) on the basis of material collected from the Falkland Islands by J. D. Hooker. Gottsche *et al*. (1847) transferred it to *Lophocolea* and Mitten (1855) found this species to be identical to *L. lenta*.

Differentiation. — The species with which *Lophocolea lenta* is most likely to be confused in Antarctica is *Clasmatocolea rigens*. It can be distinguished from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that species by its convex, rectangular to narrowly ovate-truncate leaves and constantly transversely oriented underleaves. In contrast, *C. rigens* has concave, widely ovate leaves and the underleaves are obliquely inserted.

Reproduction in Antarctica. — Fertile plants unknown.

Habitat. — On heated ground around fumaroles or on rocky ground.

World range. — *Lophocolea lenta* is a cool south-temperate species having a bicentric amphipacific distribution in the Southern Hemisphere (Fig. 75). In the Australasian sector it is known from New Zealand, SE Australia and Tasmania as well as from periantarctic Southern Ocean islands including Snares Island, Auckland Islands and Campbell Islands, and subantarctic Macquarie Island. In the South American sector it occurs on South Georgia, the Falkland Islands including Beauchêne Island (Lewis Smith & Prince, 1985), Tierra del Fuego and in the *Nothofagus* zone in Western Patagonia extending northwards to the Valdivian Province, and southwards to the South Sandwich and South Orkney Islands in the maritime Antarctic (Grolle, 1972*a*; Fulford, 1976; Engel, 1978, 1990*a*).

Distribution in Antarctica. — A very rare species known only from one small island in the South Sandwich and South Orkney Islands archipelagoes; at the former site it is frequent at elevations of 100–200 m (Fig. 76).

Specimens examined. — SOUTH SANDWICH ISLANDS. **LESKOV ISLAND**. Summit ridge, 100 m, *Convey 245L, 249J & 250E* (AAS, KRAM) and 200 m, *Longton 483A, 485C, 487B, 490B, 498B, 499, 500B, 507B & 515B* (AAS, KRAM).

SOUTH ORKNEY ISLANDS. **LAURIE ISLAND**. Cerro Diabel, 150 m, Dec 1962, *Bellisio s.n.* (BA).

Literature records. — SOUTH SANDWICH ISLANDS: without indication of the island (Lewis Smith, 1993: 322 as *Lophocolea secundifolia*); Leskov Island (Grolle, 1972*a*: 84 as *Lophocolea secundifolia*; Fulford, 1976: 477; Longton & Holdgate, 1979: 10 as *L. secundifolia*; Ochyra & Váňa, 1989*b*: 218).

4. PACHYGLOSSA HERZOG & GROLLE

Pachyglossa Herzog & Grolle, Rev. Bryol. Lichénol. **27**: 150. 1959 ["1958"]. – HOLOTYPE: *Pachyglossa tenacifolia* (Hook. f. & Taylor) Herzog & Grolle (*Jungermannia tenacifolia* Hook. f. & Taylor).

Plants very small to medium-sized, subisophyllous, in loose or dense tufts, patches or mats, brownish-green, yellowish- or reddish-brown, brownish or reddish to blackish. *Stems* from 3 mm to 8 cm long, simple or sparsely lateral-intercalary to ventral-intercalary branched, with

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FIGURE 74. *Lophocolea lenta*. **1**. Sterile shoot, lateral view. **2**. Portion of main shoot, ventral view. **3–8**. Leaves. **9–12**. Underleaves. **13**. Cells at leaf lobe. **14**. Mid-leaf cells. **15**. Cells of amphigastrium. **16**. Transverse section of stem. **17–20**. Gemmae. (All from *Longton 499*, AAS.) Scale bars: a – 100 µm (13–15); b – 1 mm (1); c – 1 mm (2); d – 1 mm (3–12) and 200 µm (16); e – 100 µm (17–20).

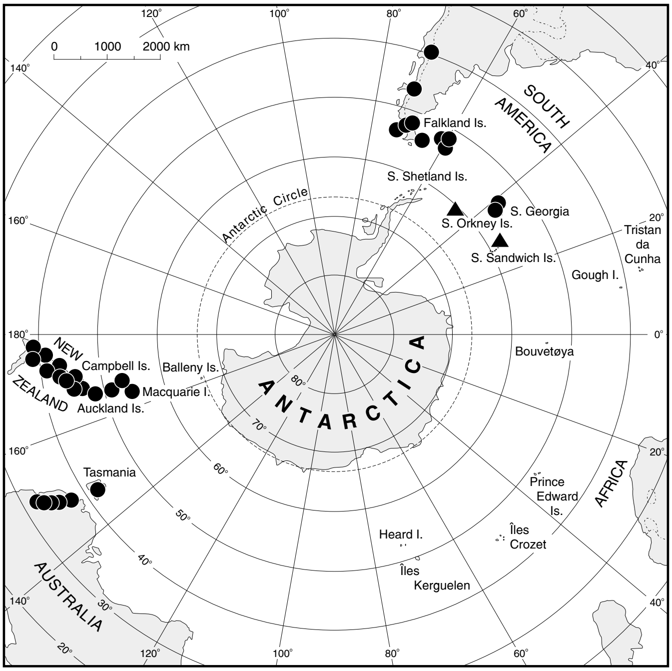

FIGURE 75. Global distribution of *Lophocolea lenta*. The Antarctic localities are indicated by triangles.

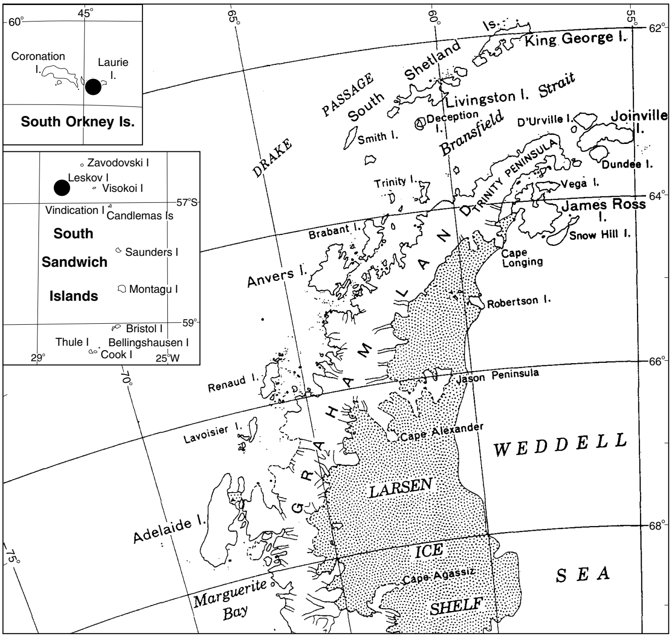

FIGURE 76. Distribution of *Lophocolea lenta* in the Antarctic.

well developed microphyllous stolons at the base, in transverse section 6–18 cells high, consisting of a distinct, 1–3-stratose cortex of smaller cells with moderately thick to strongly incrassate, brownish walls surrounding somewhat larger, hyaline medullary cells with small trigones. *Rhizoids* infrequent, arising from stolons and flagelliform branches. *Leaves* transversely or subtransversely inserted, 0.1–1.2 mm long, distant or subimbricate, ligulate, obovate, ovate or broadly ovate to nearly circular, thick, pluristratose throughout or occasionally bistratose only in the lower half, broadly obtuse or bluntly acute, entire or retuse to shallowly bilobed at the apex; leaf cells quadrate to short-rectangular becoming elongate basally, 10–20 × 10–35 μm wide, thin-walled or with slightly evenly thickened walls, mostly without trigones. *Underleaves* similar to lateral leaves, but slightly smaller, rigidly patent. *Dioecious*. *Male inflorescenses* terminal, becoming intercalary on the stem or branches; male bracts and bracteoles similar to the leaves and underleaves only somewhat larger, monandrous; antheridial stalk 1–3-seriate. *Female inflorescence* terminal; female bracts and bracteoles in 2–3 rows, similar to the leaves and underleaves, but larger. *Perianth* trigonous, 4–5-plicate above, with trilobed mouth. *Sporophytes* unknown.

A small subantarctic genus of four species distributed predominantly on all subantarctic islands, extending northwards into the cool temperate region in the *Nothofagus* zone in southern South America north to the Valdivian Province in Chile, Tristan da Cunha and the Auckland Islands and Stewart Island in the Australasian sector, but only at high elevation, and southwards to the northern maritime Antarctic. An apparently unpublished record of *Pachyglossa tenacifolia* is known from New Zealand (South Island, Denniston Plateau, lat. 42°S, 850 m, immersed in quick flowing stream on rocks growing with *Blindia immersa*, 1980, *Bartlett 196*, JE) and it indicates that the genus also extends farther north in the Australasian sector.

Pachyglossa was formally described by Herzog and Grolle (1958) who placed in it three species, *P. tenacifolia* (Hook. f. & Tayl.) Herzog & Grolle from the New Zealand sector, and *P. dissitifolia* Herzog & Grolle and *P. spegazziniana* (C. Massal.) Herzog & Grolle from the South American sector, the latter with two varieties. Later, Grolle (1958) added a fourth species, *P. fissa* (Mitt.) Grolle, from Îles Kerguelen. However, the name *Pachyglossa* appeared twice prior to its valid publication in the papers of Martin (1950) and Herzog (1952*c*).

The genus is distinct and readily distinguished by its multistratose leaves. Fulford (1963*a*) established the separate family Pachyglossaceae to accommodate it but this concept has not gained wide acceptance (Schuster, 1979*a*, 1984; Grolle, 1983*a*).

Pachyglossa is retained here in the Geocalycaceae according to the original suggestion of Herzog and Grolle (1958). Although species of *Pachyglossa* are not prominent constituents in the impoverished Antarctic liverwort flora, it is the largest genus of hepatics in this region, comprising three species, two of which are newly recorded from Antarctica. They represent three different sections of the genus, namely sect. *Pachyglossa* (*P. dissitifolia*), sect. *Fissae* (*P. fissa*) and sect. *Spegazzinianae* (*P. spegazziniana*). These are recognised in the following key.

Key to the Antarctic species of *Pachyglossa*

1\. Leaves unistratose in the upper part, bistratose only in the basal portion; superficial leaf cells 10–16 × 10–20 µm . . . . **3. *P. spegazziniana*** var. ***exilis***

1\. Leaves pluristratose throughout; superficial leaf cells 15–20 × 15–35 µm 2

  2\. Leaves ligulate to ovate . . . . **1. *P. dissitifolia***

  2\. Leaves broadly ovate . . . . **2. *P. fissa***

1. *Pachyglossa dissitifolia* Herzog & Grolle — Fig. 77

Pachyglossa dissitifolia Herzog & Grolle, Rev. Bryol. Lichénol. **27**: 155, *f. 2–3*. 1959 ["1958"] [*Pachyglossa dissitifolia* Herzog, Rev. Bryol. Lichénol. **21**: 259, *f. 3a–f.* 1952, *comb. inval.*]. – Type: [Chile, Prov. Aisén] Westpatagonien, Cerro-Tesoro-Massiv, ca. 1.000 m, leg. G. H. Schwabe, 1940 [Holotype: "Herbarium Haussknecht, Jena Pachyglossa ~~stenophylla~~ dissitifolia Herz. n. sp. Fl. v. Westpatagonien Cerro-Tesoro-Massiv *ca* 1000 m leg. G. H. Schwabe, 13.2.40 no. 39c, pp" – JE-herzog!].

Plants small to medium-sized, slender, flaccid, in loose or dense tufts or mats, or scattered amongst bryophytes, dull, bright to dark, green, brownish-green to brownish. *Stems* erect or suberect, to 5 cm long, rigid, lateral-intercalary to ventral-intercalary branched, with rare microphyllous stolons, in transverse section with a 1(–2)-stratose cortex, of somewhat smaller cells with brownish and incrassate walls and medulla with larger leptodermous cells with small trigones. *Rhizoids* relatively rare, clustered on stolons. *Leaves* subtransversely or transversely inserted, distant to loosely imbricate, narrowly ovate to ligulate, 0.2–0.8 mm long, 0.3–0.4 mm wide, fleshy, pluristratose throughout, entire-margined, obtuse, slightly retuse to shallowly (0.1–0.2) bilobed, concave to canaliculately concave; leaf cells 15–35 × 15–25 µm in surface view, with slightly uniformly thickened walls, without or with minute trigones; cuticle verrucose. *Underleaves* similar to leaves, but slightly smaller, mostly very shallowly bifid. *Sterile* in Antarctica.

Taxonomic and nomenclatural notes. — Although *Pachyglossa dissitifolia* is the commonest of all species in the genus, it was first collected in 1940 by G. H. Schwabe in Western Patagonia. Herzog (1952*c*) described it in detail but this name was invalid because the genus was then invalidly published. It was later validated by Herzog and Grolle (1958).

Differentiation. — A very characteristic, small species known by its radially symmetric appearance because of the subisophyllous foliage and fleshy, ovate to ligulate, mulstistratose leaves with entire or slightly bilobed leaf apices.

Reproduction in Antarctica. — Fertile plants unknown.

Habitat. — It grows most often on gravelly soil in moist, exposed or sheltered sites, often as a pioneer species; also on wet ground around fumaroles, on peaty soil, scree, moss banks, rock outcrops, in rock crevices, on ledges and rocks supplied with trickling melt water, often in late snow patches, mostly associated with

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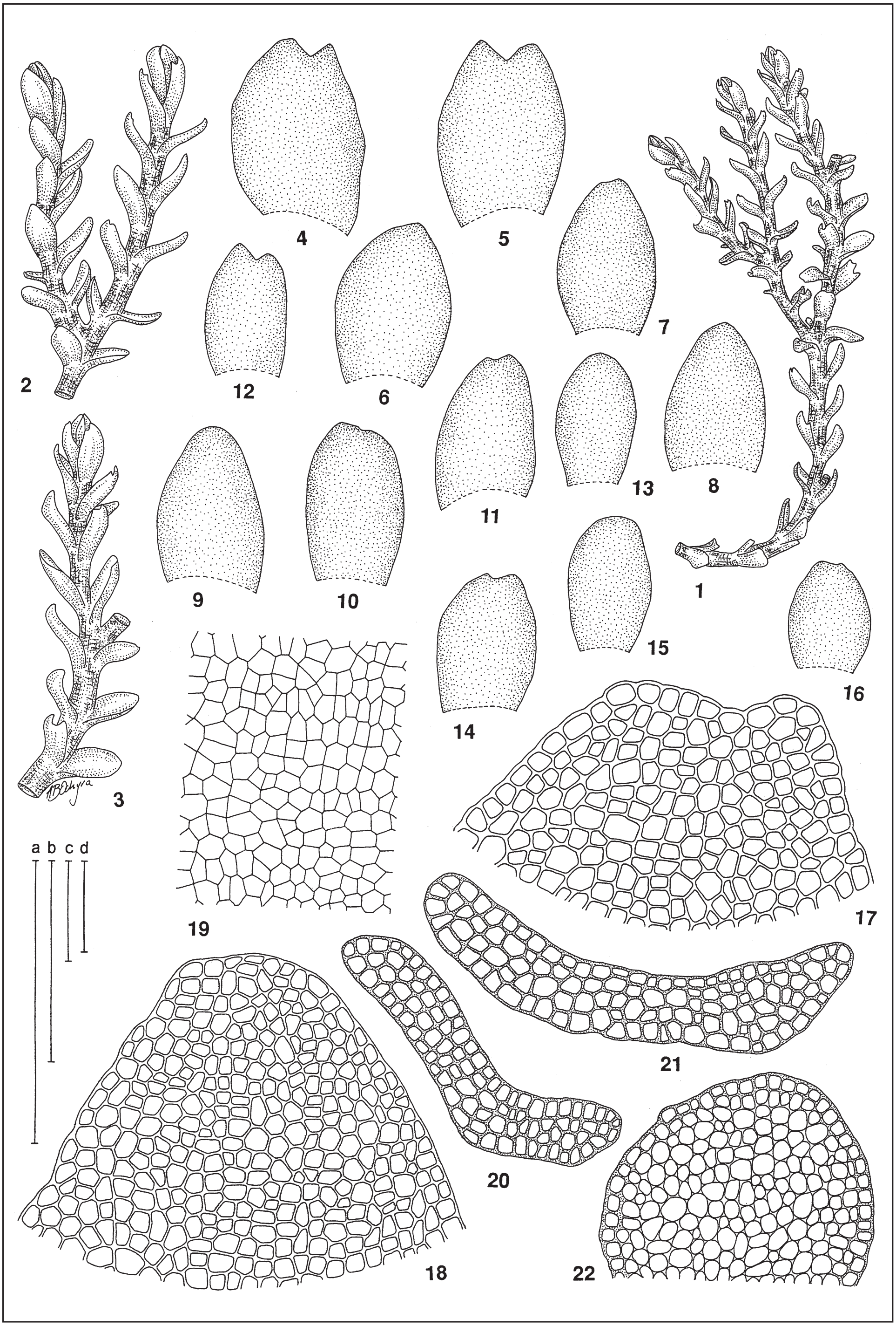
Figure 77. *Pachyglossa dissitifolia*. **1–3**. Sterile shoots. **4–11**. Leaves. **12–16**. Underleaves. **17–18**. Cells at leaf apices. **19**. Areolation of mid-leaf. **20–21**. Transverse sections of leaves. **22**. Transverse section of stem. (All from *Ochyra 2005/80*, KRAM.) Scale bars: a – 5 mm (1); b – 1 mm (4–16); c – 100 µm (17–22); d – 1 mm (2–3).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Anthelia juratzkana, *Andreaea* spp. and *Polytrichastrum alpinum*. It has been found associated with *Warnstorfia sarmentosa* and *Drepanocladus longifolius* on Byers Peninsula, Livingston Island, growing submerged in Midge Lake at *ca* 1–2 m depth.

World range. — An American subantarctic species known from South Georgia, the northern maritime Antarctic, Bouvetøya, and on Tristan da Cunha and Gough Island, the Falkland Islands and Tierra del Fuego extending as far north as the Valdivian Province. Outside the subantarctic region it occurs at high elevations, mainly between 1000–1500 m, extending to 2000 m on Tristan da Cunha (Grolle, 1958, 1969; Schuster, 1974; Engel, 1990*a*) (Fig. 78).

Distribution in Antarctica. — The most frequent species of the genus, known exclusively from the northern maritime Antarctic including Bouvetøya, South Sandwich Islands, South Orkney Islands and South Shetland Islands, extending as far south as Melchior Islands in the Palmer Archipelago near the western coast of the Antarctic Peninsula at lat. 64°20'S (Fig. 79). It usually occurs from sea level to *ca* 250 m (exceptionally to 600 m).

Specimens examined. — BOUVETØYA. Rustadkollen, 323 m, *Engelskjøn 36* (AAS) and 300–340 m, *Engelskjøn 224, 227, 234, 245 & 411* (BG); nunatak east of Rustadkollen, 290 m, *Engelskjøn 100* (BG); Moseryggen, 260–287 m, *Engelskjøn 310 & 405* (BG).

SOUTH SANDWICH ISLANDS. **Leskov Island**. Summit ridge, 200 m, *Longton 483B* (AAS, KRAM); south end of summit ridge, *ca* 200 m, *Holdgate 835B* (AAS, KRAM).

SOUTH ORKNEY ISLANDS. **Coronation Island**. Olivine Point, *ca* 35 m, *Lewis Smith 133 & 142* (AAS, KRAM). **Lynch Island**. Without specific locality, *ca* 17 m, *Lewis Smith 532A* (AAS, KRAM). **Matthews Island**. North-west coast, 50 m, *Lewis Smith 162* (AAS, KRAM). **Powell Island**. West of John Peaks, *ca* 35 m, *Lewis Smith 260* (AAS, KRAM); above north-west coast, 600 m, *Lewis Smith 241* (AAS, KRAM); east coast, *ca* 135 m, *Lewis Smith 225B* (AAS, KRAM). **Signy Island**. Jane Peak (between summit and Knob Lake), 50 m, *Lewis Smith 10799* (AAS, KRAM); Factory Cove, 50 m, *Longton 852* (AAS, KRAM), 85 m, *Lewis Smith 5199* (AAS, KRAM) and without elevation, *Lewis Smith 1837* (AAS, KRAM); Moraine Valley, 50 m, *Lewis Smith 411A* (AAS, KRAM), 60 m, *Lewis Smith 5225* (AAS, KRAM), 75 m, *Lewis Smith 5198B* (AAS, KRAM) and 85 m, *Lewis Smith 5025B* (AAS, KRAM); Observation Bluff, 50 m, *Lewis Smith 321* (AAS, KRAM); Polynesia Point, 50 m, *Lewis Smith 10744* (AAS, KRAM); west slope of Rusty Bluff, *ca* 50 m, *Lewis Smith 542B* (AAS, KRAM); south of Berntsen Point, *ca* 35 m, *Lewis Smith 539B* (AAS, KRAM). **Moe Island**. 150–200 m, *Lewis Smith 5257* (AAS, KRAM).

SOUTH SHETLAND ISLANDS. **King George Island**. ***Admiralty Bay***: Jersak Hills, 200 m, *Ochyra 5118/79* (AAS, KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 125]; Italia Valley, 100 m, *Ochyra 88A/80* (KRAM, PRC); Urbanek Crag, 120 m, *Ochyra 2346/80* (KRAM, PRC) and 130 m, *Ochyra 2333/80* (KRAM, PRC); Komandor Peak, 250 m, *Ochyra 1936A/80* (KRAM, PRC); Wegger Peak, 300 m, *Ochyra 2005/80* (KRAM, PRC) [*Bryophyta Antarctica Exsiccata* No. 25] and 320 m, *Ochyra 1997/80* (KRAM, PRC); Kapitan Peak, 190 m, *Ochyra 1904/80* (KRAM, PRC) and 200 m, *Ochyra 1913/80* (KRAM, PRC); Mt. Wawel, 40 m, *Ochyra 2159/80* (KRAM, PRC). ***Fildes Peninsula***: Bellingshausen Station, 15 m, *Ochyra 2411/80* (KRAM, PRC); without specific locality,

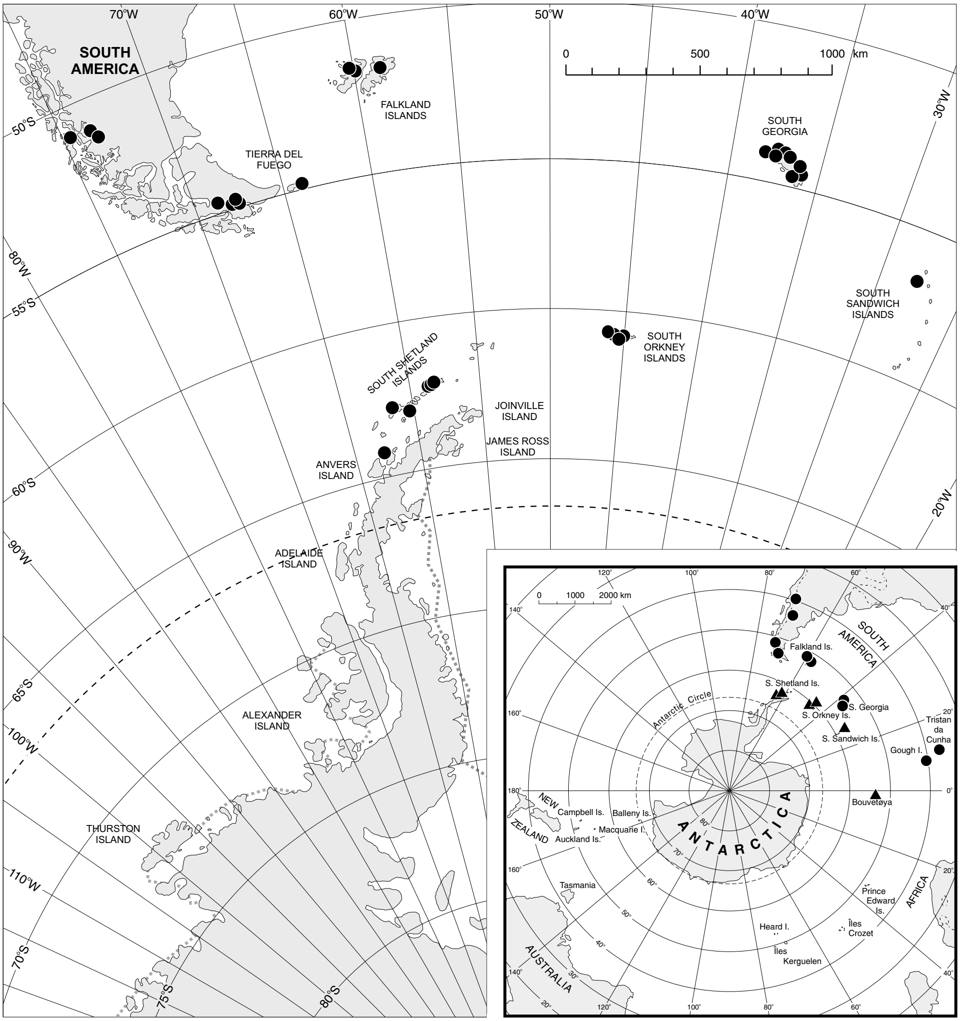

FIGURE 78. Distribution of *Pachyglossa dissitifolia* in the Antarctic and Fuegian region. Inset: global distribution. The Antarctic localities are indicated by triangles.

14 Jan 1989, *Li BA20* (AAS). LIVINGSTON ISLAND. ***Byers Peninsula***: Midge Lake south of Chester Cone, 30 m, *Lewis Smith 3831* (AAS). ***Hurd Peninsula***: South Bay, Mt. Reina Sofia, 260 m, *Schulz 77* (Hb. Schulz, KRAM).

WEST ANTARCTIC PENINSULA. **DANCO COAST**. ***Melchior Islands***: Gamma Island, 5–10 m, *Lewis Smith 4154 & 4155* (AAS, KRAM).

Literature records. — BOUVETØYA: Rustadkollen and Moseryggen (Engelskjøn, 1981: 19, 21; 1987: 145, 161; Bell & Blom, 1986: 12; Engelskjøn & Jørgensen, 1986: 74; Ochyra & Váňa, 1989*b*: 217). SOUTH SANDWICH ISLANDS: Leskov Island (Grolle,

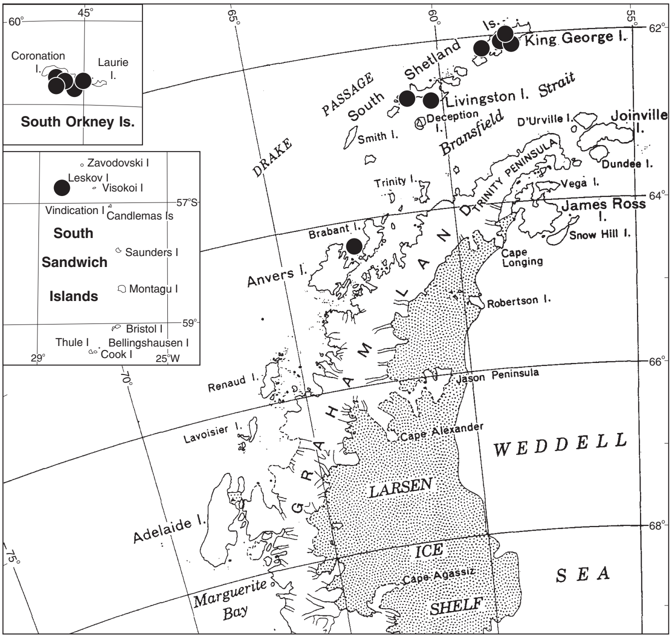

FIGURE 79. Distribution of *Pachyglossa dissitifolia* in the maritime Antarctic.

1972*a*: 85; Longton & Holdgate, 1979: 11: Ochyra & Váňa, 1989*b*: 218). SOUTH ORKNEY ISLANDS: Coronation Island (Ochyra & Váňa, 1989*b*: 218); Lynch Island (Bonner & Lewis Smith, 1985: 82); Powell Island (Bonner & Lewis Smith, 1985: 91; Ochyra & Váňa, 1989*b*: 218); Signy Island (Lewis Smith, 1972: 19, 28; 1987: 242; Smith & Gimmingham, 1976: 36; Lewis Smith & Coupar, 1986: 194; Ochyra & Váňa, 1989*b*: 218). SOUTH SHETLAND ISLANDS: King George Island (Ochyra *et al.* 1982: 261; 1986: 55; Ochyra, 1984: 6, 18; Ochyra & Váňa, 1989*a*: 205; 1989*b*: 218; Okada & Kanda, 1994; Chen *et al.*, 1985: 140–142; Li *et al.*, 1998*a*: 201 both as *Cephalozia bicuspidata*); Livingston Island (Schuster, 1969*a*: 103; 1979: 2211; Ochyra & Váňa, 1989*b*: 218; Sancho *et al.*, 1999: 322). ANTARCTIC PENINSULA: Danco Coast (Ochyra & Váňa, 1989*b*: 218).

2. *Pachyglossa fissa* (MITT.) HERZOG & GROLLE FIG. 80

Pachyglossa fissa (Mitt.) Herzog & Grolle *in* Grolle, Rev. Bryol. Lichénol. **28**: 346. 1959 [“1958”]. – *Herpocladium fissum* Mitt., J. Linn. Soc. Bot. **15**: 69. 1876. – TYPE: Kerguelen’s Island [HOLOTYPE: NY-MITT!].

Plants very small (in Antarctica), gregarious, only to 3–5 mm long, brownish. *Stems* simple or sparingly lateral-intercalary or ventral-intercalary branched, with stolons at the base, rigid, in cross-section 13–15 cells high, cortical cells in 1–2 layers, smaller, with slightly thickened,

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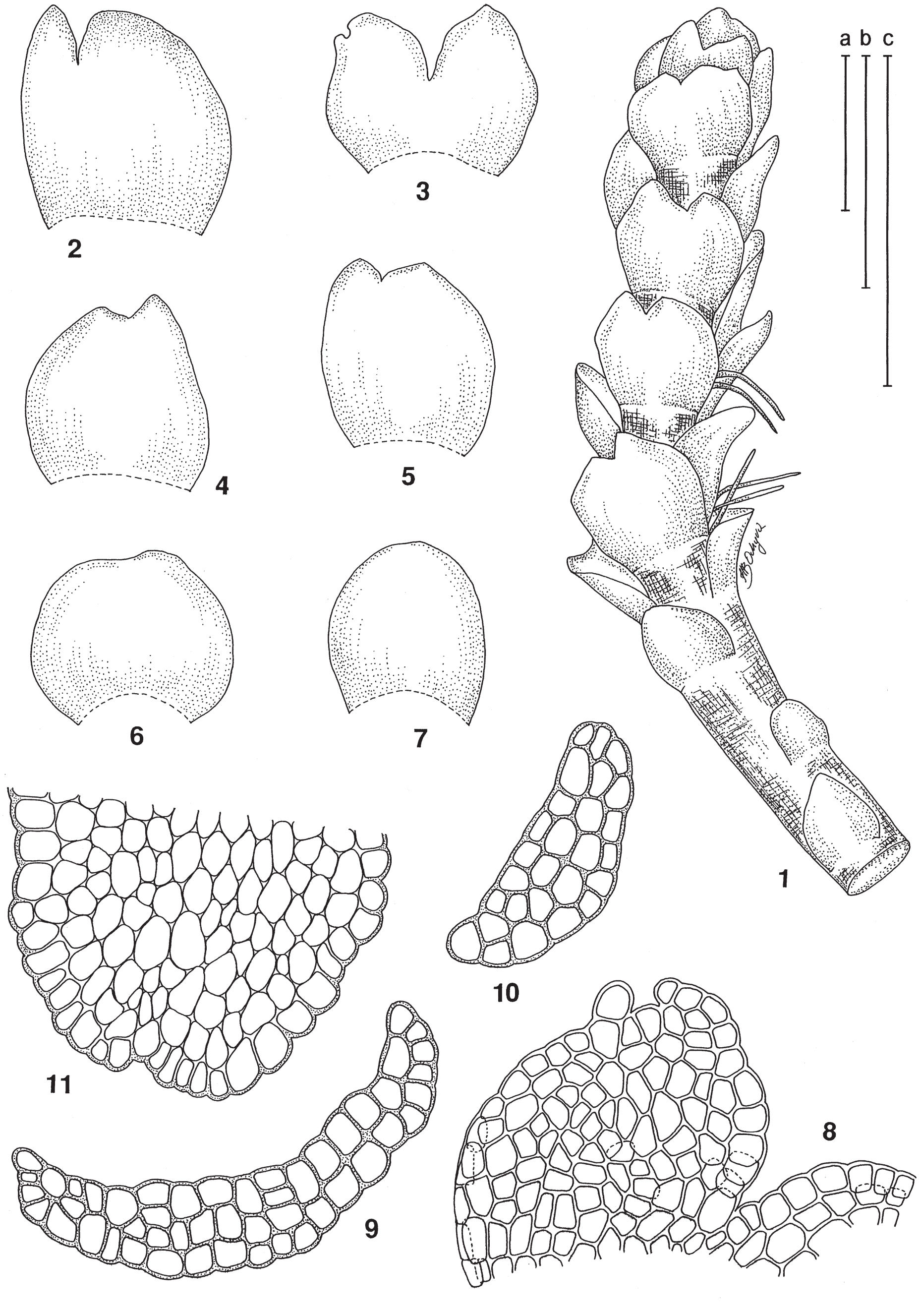
FIGURE 80. *Pachyglossa fissa*. **1**. Sterile shoot, lateral view. **2–6**. Leaves. **7**. Underleaf. **8**. Cells at leaf apex. **9**. Transverse section of leaf in upper two thirds. **10**. Transverse section of leaf lobe. **11**. Transverse section of stem portion. (All from *Lewis Smith 425*, AAS.) Scale bars: a – 100 µm (8–11); b – 0.5 mm (1); c – 0.5 mm (2–7).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brownish walls; medullary cells somewhat larger, leptodermous, with minute trigones. *Rhizoids* rare, arising from the bases of scale-like leaves on stolons. *Leaves* nearly transverse or slightly succubous, erect-spreading, fleshy, 0.2–0.4 mm long, 3–5-stratose in transverse section throughout, broadly ovate, obtuse, retuse or bilobed to 0.1–0.2 of the length at the apex; sinus narrow; lobes rounded to subacute; margins entire; leaf cells slightly thick-walled, with tiny trigones, 15–25 µm in diamater. *Underleaves* similar to leaves, more commonly acute, not broadly rounded at the apex, sometimes variously retuse or bilobed. *Sterile* in Antarctica.

Taxonomic and nomenclatural notes. — The species was described from Îles Kerguelen by Mitten (1876) as *Herpocladium fissum* and retained that name until Grolle (1958) proposed its current generic placement.

Differentiation. — *Pachyglossa fissa* maybe recognised by its broadly ovate, obtuse leaves which are distinctly bilobed or retuse at the apex. The Antarctic plants are exceedingly small in contrast to those from more northerly latitudes, where they attain 2 cm in height.

Reproduction in Antarctica. — Fertile plants unknown.

Habitat. — In relatively dry rock crevices.

World range. — An amphiatlantic subantarctic species, known from several subantarctic islands (Heard Island, Îles Kerguelen, Prince Edward Islands, South Georgia) and widely distributed but scattered at high elevations in southern South America from Tierra del Fuego to the Valdivian Province, on the Falkland Islands (Grolle, 1958, 1969, 1971*a*; Fulford, 1963*a*; Gremmen, 1982; Engel, 1990*a*; Bergstrom & Selkirk, 1997), and extending to the South Orkney Islands in Antarctica (Fig. 81).

Distribution in Antarctica. — Recorded from a single specimen in the South Orkney Islands (Fig. 81). This is the first record of this species in Antarctica.

Specimens examined. — SOUTH ORKNEY ISLANDS. SIGNY ISLAND. East side of Rusty Bluff above Paal Harbour, *ca* 85 m, *Lewis Smith 425* (AAS, KRAM).

Literature records. — None.

3. ***Pachyglossa spegazziniana*** (C. MASSAL.) HERZOG & GROLLE var. ***exilis*** HERZOG & GROLLE FIG. 82

Pachyglossa spegazziniana (C. Massal.) Herzog & Grolle var. *exilis* Herzog & Grolle, Rev. Bryol. Lichénol. **27**: 159. 1958. – *P. exilis* (Herzog & Grolle) Hässel & Solari *in* Boelcke, Moore & Roig, Trans. Bot. Patag. Austr.: 324. 1985. – TYPE: 1. Tierra del Fuego; in alpinis supra ostium fluminis Azopardo, 720 m., leg. T. Halle et C. Skottsberg, 1908, in Hb. Uppsala. 2. Chile: Vulcan Calbuco (Ostseite), ca 1.000 m., leg. W. Schiller, 1922, in Hb. Herzog. 3. Westpatagonien: Cerro-Tesoro-Massiv, ca 1.000 m., leg. G. H. Schwabe, 1940, in Hb. Herzog. 4. Isla de los Stados, P. Cook. leg. C. Skottsberg, 1903, in Hb. Stockholm. 5. Falkland-Inseln: Mt. Adam, 700 m., leg. I. Halle et C. Skottsberg 1908, in Hb. Uppsala und Genf (Typus von *Herpocladium minimum*). 6. Tristan da Cunha: Above Burntwood, rock crater, 600 und 1.200 m., leg. Christophersen and Mejland, 1938, in Hb. Stockholm. 7. Tristan da Cunha: The Peak, in shelter, 2.000 m. leg. Christophersen and Mejland, 1938, in Hb. Stockholm [LECTOTYPE (*fide* Hässel de Menendez & Solari, 1985: 325): Falkland Islands, Mt. Adam, 700 m, leg. Skottsberg & Halle – UPS (*non vidi*); ISOLECTOTYPE; JE!; SYNTYPES (all): JE!].

Plants very small, to 4 mm long, prostrate to ascending, gregarious, yellowish-brown to brownish. *Stems* simple or sparsely, mostly ventral-intercalary, branched, rigid and fleshy, in

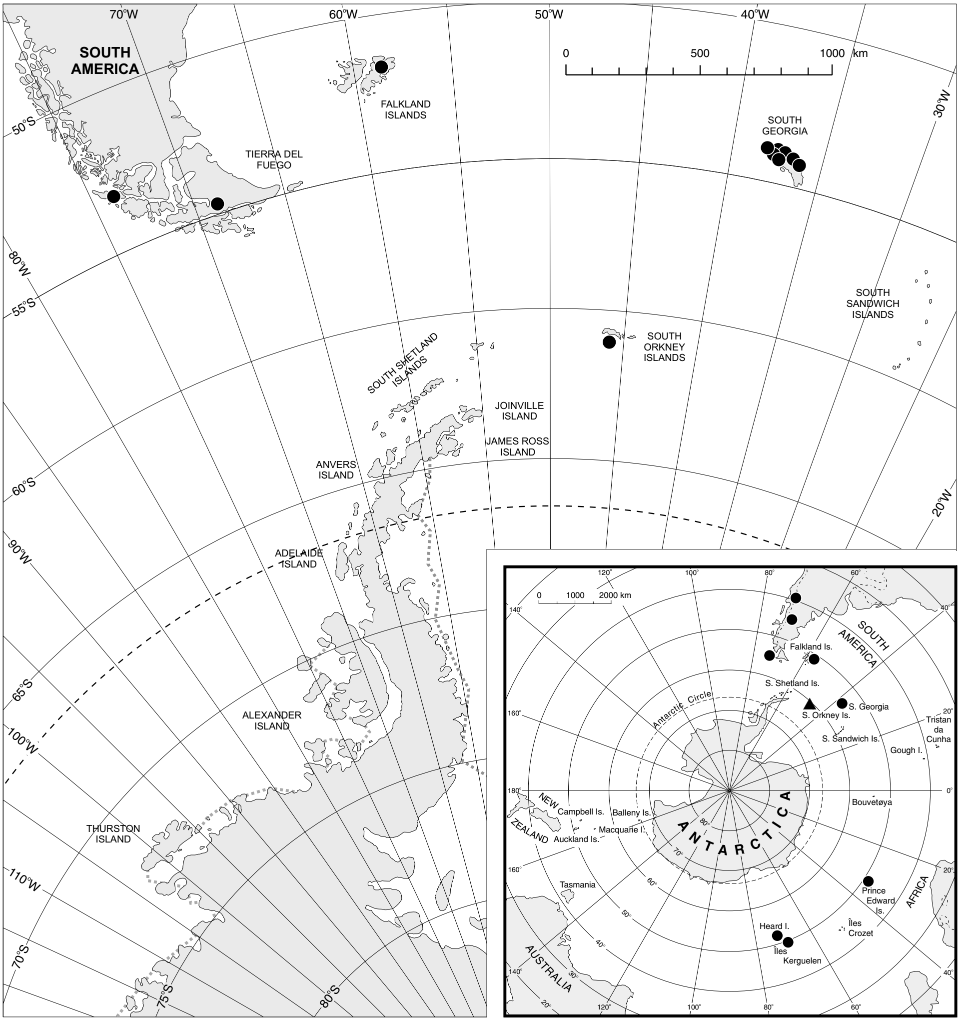
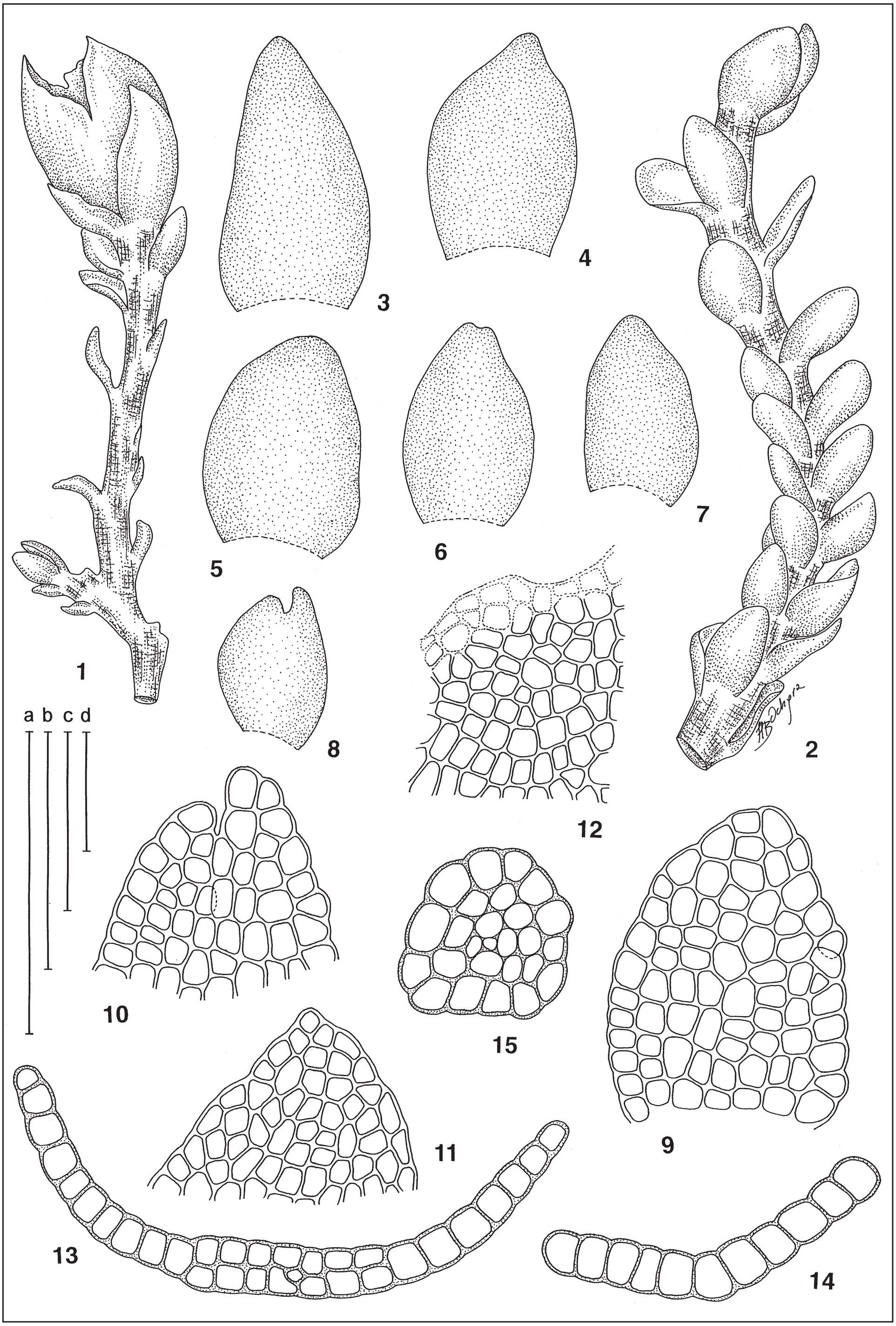


FIGURE 81. Distribution of *Pachyglossa fissa* in the Antarctic and Fuegian region. Inset: global distribution. The Antarctic locality is indicated by a triangle.

transverse section 6–8 cells high, with a unistratose cortex of large, thick-walled cells, nearly equal to the internal, thinner-walled cells, with small trigones. *Rhizoids* rare. *Leaves* nearly transverse or slightly succubous, 0.1–0.4 mm long, erecto-patent, distant to approximate, broadly ovate to elliptic, broadly rounded and obtuse, very rarely slightly retuse at the apex, entire-margined, unistratose distally, bistratose only in central part of the basal portion; leaf cells mostly thin-walled, 10–20 × 10–18 µm. *Underleaves* similar to the leaves only somewhat smaller, subacute, rarely slightly bilobed; cuticle smooth. *Dioecious* (only one perianth-bearing plant seen). *Female inflorescence* terminal; bracts larger than the leaves but otherwise similar. *Perianth* ovoid, obscurely 3-keeled, lobate at the mouth. *Remainder* unknown.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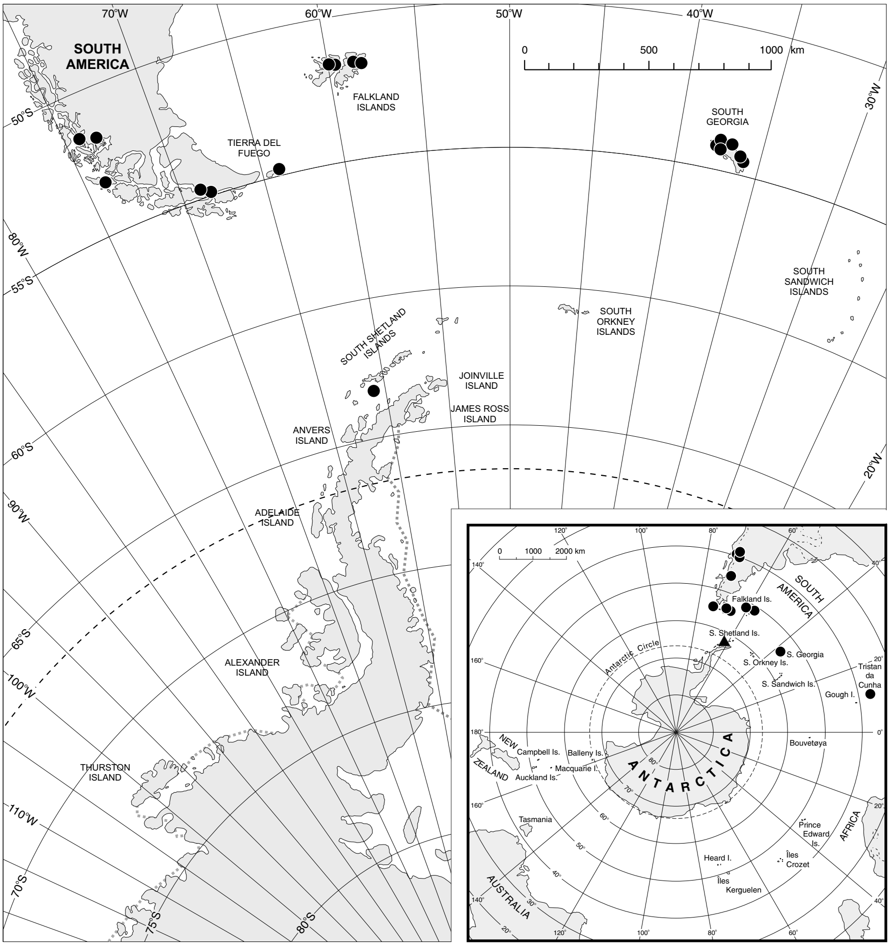

FIGURE 83. Distribution of *Pachyglossa spegazziniana* in the Antarctic and Fuegian region. Inset: global distribution. The Antarctic locality is indicated by a triangle.

Taxonomic and nomenclatural notes. — *Pachyglossa spegazziniana* is generally a large though slender plant which, in extreme cases, may reach 8 cm. However, most plants are represented by small phenotypes; these were recognised by Herzog and Grolle (1958) as var. *exilis*. Stephani had intended to describe such

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FIGURE 82. *Pachyglossa spegazziniana* var. *exilis*. **1**. Shoot with immature perianth, lateral view. **2**. Sterile shoot, dorsal view. **3–6**. Leaves. **7–8**. Underleaves. **9**. Leaf cells. **10–11**. Leaf apices. **12**. Cells at perianth mouth. **13–14**. Transverse section of leaves. (All from *Mason 119E*, AAS.) Scale bars: a – 0.5 mm (2); b – 1 mm (1) and 100 µm (13–15); c – 100 µm (9–12); d – 100 µm (3–8).

small phenotypes from the Falkland Islands as *Herpocladium minimum*, but this name has remained unpublished. Fulford (1963*a*) considered var. *exilis* to be merely a small and simplified facies of *P. spegazziniana* and reduced this name to synonymy. However, Hässel de Menendez and Solari (1985) considered the size of the plants to be sufficient for distinction of this variety as a species in its own right, and formally elevated it to species. Although the systematic value of this variety is doubtful, because it is probably only a response to harsh enviromental conditions, we accept the original concept of Herzog and Grolle (1958), as Engel (1990*a*) did with the Falkland Islands plants, and retain the variety as a separate taxon in order to emphasize the small stature of the Antarctic plants.

Differentiation. — It may be separated from other species of *Pachyglossa* by its partially unistratose leaf lamina in the distal part and by being only bistratose in the lower half.

Reproduction in Antarctica. — Fertile plants unknown, although female plants with normal perianths have been found.

Habitat. — On volcanic ash and scoria in geothermal area.

World range. — A subantarctic amphiatlantic species known from South Georgia in the sub-Antarctic and widely distributed, though infrequent, on the Falkland Islands and on mainland southern South America from Tierra del Fuego to the Valdivian Province, at altitudes mostly above 600 m in Tierra del Fuego and between 1400 and 1700 m in the Valdivian Andes. Additionally, there is a very isolated and disjunct occurrence of this species on Tristan da Cunha at 2000 m, and also in the Antarctic (Herzog & Grolle, 1958; Fulford, 1963*a*; Engel, 1990*a*) (Fig. 83).

Distribution in Antarctica. — Known from a single specimen from the volcanic Deception Island in the South Shetland Islands at an elevation of 350 m (Fig. 83).

Specimens examined. — SOUTH SHETLAND ISLANDS. **DECEPTION ISLAND**. Summit peak 2.2 km WNW of Mt. Kirkwood, 350 m, *Mason 119E* (AAS, KRAM).

Literature records. — None.

GEOCALYCACEAE SPECIES EXCLUDED FROM ANTARCTICA

Lophocolea willii Grolle. — This species was first described by Grolle (1972*a*) from material from South Georgia and southern South America. Fulford (1976) also reported one station from the Antarctic, namely "South Sandwich Islands: Leskov Ridge, *Longton* (BIRM)" and referred this record to Grolle (1972*a*). This is evidently an erroneous record since Grolle (1972*a*) did not cite this species from the archipelago; this specimen correctly refers to *Lophocolea lenta* which was cited from Leskov Island on the basis of the specimens collected by R. E. Longton.

Order **II. METZGERIALES** R. M. SCHUST. *EX* SCHLJAKOV

Metzgeriales R. M. Schust. *ex* Schljakov, Bot. Zhurn. **57**: 500. 1972 [Metzgeriales Underw., Bot. Gaz. **19**: 356 361. 1894; Chalaud, Ann. Bryol. **3**: 41. 1930, *nom. nud.*; R. M. Schust., Am. Midl. Nat. **49**(2): 285. 1953, *inval. sine descr. lat.*].

Plants thallose or occasionally nearly foliose, strongly dorsiventral, furcate or pinnate, with an apical cell with 2(–3) cutting faces, usually formed of simple parenchymatic cells, without air-chambers and pores on the dorsal surface; internal tissue without or with few chloroplasts, not differentiated into upper chlorophyllose and lower parenchymatous layers; epidermal cells unistratose, mostly thin-walled and without trigones, with chloroplasts (except in *Cryptothallus*), cuticle smooth; oil-bodies few and large to many and small; midrib not or well defined, plano-convex, biconvex or concavo-convex, variously differentiated or undifferentiated. *Rhizoids* simple, smooth, continuous along the ventral surface of midrib. *Ventral scales* delicate and ephemeral, in 1 row on each side of midrib, or lacking. *Asexual reproduction* often by 1–2- to multicellular gemmae or by small caducous branches. *Female inflorescences* never terminal, produced continuously on the dorsal surface or on short lateral or ventral branches. *Sporophyte* with a distinct foot, protected by flap-like or cylindrical pseudoperianth or by scales when developing; seta mostly unspecialised; capsule globose, ellipsoid to cylindrical; capsule walls 2–4-stratose, splitting into 2–4(–6) valves. *Spores* uni- or multicellular, usually more than 20 µm in diameter, often papillose or areolate; elaterophores sometimes present at base or apex of capsule.

This order shows a greatest diversity in morphology of the gametophores, ranging from a clearly thallose condition to one that is essentially leafy. Because in most individuals the archegonia are lateral, this group was called “Jungermanniales anacrogyne” in the older literature, but this term is nomenclaturally aberrant. Additionally, not all taxa are anacrogynous, i.e. a lateral cell does not always initiate archegonium production. The Metzgeriales are distinguished from the Marchantiales by the absence of the internal differentiation of the thallus and by the smooth rhizoids.

The Metzgeriales contain 12 families with 32 genera (Grolle, 1983*a*) and approximately 550 species, although according to Schuster (1992*a* the accurate number is probably below 300 species. They are mostly epigean plants, some are epiphytic and one or two are subterranean saprophytes. They have a global distribution with the greatest diversity and abundance in the humid subtropics and tropics and they are sparingly found in arctic and strongly subantarctic regions. In the Antarctic this order is poorly represented, with only two species belonging in two families so far detected. These families are separated in the following couplet.

KEY TO THE ANTARCTIC FAMILIES OF METZGERIALES

1. Thallus not divided into unistratose wings and central narrow costa; setose hairs never present on the wings . . . . **X. Aneuraceae**
1. Thallus divided into unistratose, wide wings and central narrow costa; setose hairs sometimes present on wings . . . . **XI. Metzgeriaceae**

Family X. ANEURACEAE H. KLINGGR.

Aneuraceae H. Klinggr., Höh. Crypt. Preuss.: 11. 1858. – TYPE: *Aneura* Dumort.

Plants thallose, prostrate, green to somewhat brownish with no trace of reddish pigmentation. *Thallus* small to medium-sized, 0.2–1.2 cm wide, simple or branched, with terminal, usually monopodial, lateral branching, branches furcate, pinnate or irregular, in transverse section pluristratose, mostly without a discrete costa; internal tissue parenchymatous, without sclerenchymatous cells and thick interlocking bands; epidermal cells large, thin-walled, with or without minute trigones; margins plane or slightly incurved, entire to sinuate, lacking cilia or hairs. *Rhizoids* rare, arising mostly over central portions of the ventral side of the basal part of thallus, rarely from thallus margin. *Asexual reproduction* by 1–2-celled, endogenous gemmae formed mostly from epidermal cells. *Dioecious* or *paroecious*. *Male branches* short, lateral, narrower than vegetative branches, linear to short-lingulate, with 2 rows of antheridia on the dorsal surface placed singly in enclosed depressions; antheridial stalk 1(–2)-seriate. *Female branches* lateral, similar to male branches, with 2 rows of naked, dorsally sessile archegonia. *Perianth* absent. *Calyptra* large, fleshy, without surrounding pseudoperianth. *Capsule* ellipsoidal, 4-valved; capsule wall bistratose; epidermal cells with thickened bands on longitudinal walls appearing on the abaxial surface as nodular thickenings; inner cells with or without semi-annular thickened bands. *Spores* relatively small, 10–25 µm, papillose or areolate; elaters unispiral, with a very broad, reddish-brown spiral; elaterophores in fascicles at the apex of capsule valves; spore/elater width ratio 1–3 : 1.

A relatively large, cosmopolitan family with four genera and about 100 species comprising two subfamilies: Vandiemenioideae with the monotypic Tasmanian genus *Vandiemenia*, and Aneuroideae with the only saprophytic liverwort genus (*Cryptothallus*, 2 species), cosmopolitan *Aneura* (5–6 species) and the largest genus, *Riccardia*, which is represented in Antarctica by a single species.

1. RICCARDIA GRAY

Riccardia Gray, Nat. Arr. Brit. Pl. **1**: 679, 683. 1821 ["Riccardius"]. – TYPE (*cons.*): *Riccardia multifida* (L.) Gray (*Jungermannia multifida* L.).

Plants thallose, small and delicate, pale to dark green, creeping, ascending to erect. *Thallus* very narrow to narrow, fleshy, often widely 1–3-pinnately branched; branches lingulate to linear, short to long, narrow, 0.2–2.0 cm wide, rounded and emarginate or truncate at the apex, with clavate, 1–2-celled slime papillae, in transverse section circular to concavo-convex, 3–10 cells high, without a discrete costa; epidermal cells thin-walled or slightly thick-walled, without trigones, with 1–3(–15) oil-bodies. *Rhizoids* scattered on the ventral side of the thallus or sometimes present on margins. *Gemmae* 1–2-celled, endogenously produced at thallus apices. *Dioecious*, *autoecious* or occasionally *synoecious*. *Male branches* variable, mostly linear, mostly with 2–8 pairs of antheridia. *Female branches* short. *Calyptra* green, fleshy, usually papillate. *Seta* usually with 2 rings of cells consisting of 12 outer and 4 inner cell rows, rarely with 3 layers of cells. *Spores* finely papillose, 10–15 µm wide; elaters unispiral, 8–10 µm wide; spore/elater width ratio mostly 1.0–1.5 : 1.

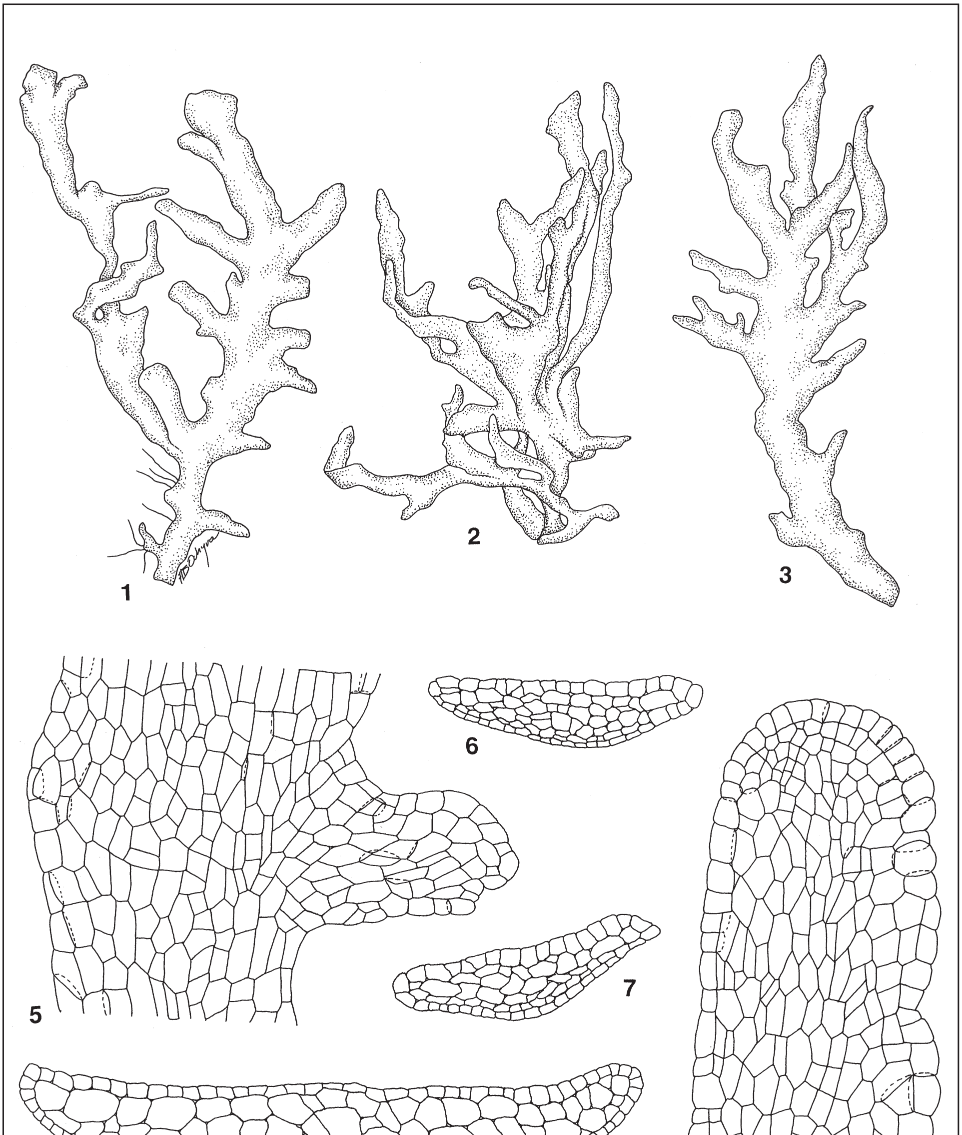
Riccardia is the largest genus in the Aneuraceae, having a wide subcosmopolitan distribution. It is still imperfectly known taxonomically, despite several good regional monographs of this genus, e.g. for Japan (Mizutani & Hattori, 1957; Furuki, 1991), Australasia (Hewson, 1970; Brown & Braggins, 1989), southern South America and adjacent areas (Evans, 1921; Hässel de Menendez, 1972), tropical Africa (Jones, 1956), the Prince Edward Islands in the Subantarctic (Schuster, 1989) and eastern North America (Schuster, 1992*a*). The number of *Riccardia* species can be estimated at 90–100. A single species, *Riccardia georgiensis*, extends into the maritime Antarctic. Moreover, gatherings of *Riccardia* should be best examined while they are fresh, when the oil-bodies are present and the thalli can be more easily sectioned. An additional problem with this genus is the great variation of the habit of the thalli and therefore poor or underdeveloped material may make determination difficult.

1. ***Riccardia georgiensis*** (STEPH.) HÄSSEL FIGS 84–85

Riccardia georgiensis (Steph.) Hässel *in* Grolle, Lindbergia **1**: 80. 1971 [“georgica”]. – *Aneura georgiensis* Steph., Wiss. Erg. Schwed. Südpol. Exp. 1901–1903, **4**(1): 2. 1905. – TYPE: South Georgia, Cumberlandbay, Borethal am Bachufer, 4.5.1902 Skottsberg [HOLOTYPE: G (*non vidi*); ISOTYPE: S!].

Plants small growing creeping or erect between mosses or forming small mats, rather firm and rigid, dark green with older thallus sectors grey-brownish. *Thalli* prostrate, to 1.0 cm long, 0.3–0.5 mm wide, without projections, ribbon-like, irregularly 1–2-pinnate, in transverse section 7–8 cells high, internally undifferentiated into layers of cells, with convex dorsal surface and flat or gently concave ventral surface, rather thick and tumid, hardly to conspicuously rounded at margins; dorsal epidermal cells thin-walled, 7–15 × 10–20 µm, clearly smaller than the large, leptodermous, 30–45 × 35–55 µm, medullary cells; cuticle slightly verruculose; ventral epidermal cells in (1–)2 layers, much smaller than medullary cells, *ca* 12–15 µm in tangential diameter, mostly 3–5 times as long as wide, sometimes mycorrhizal, forming a conspicuous ventral median band occupying 0.6–0.8 the thallus width; pinnae ascending or prostrate, 0.6–0.7 mm wide, often short and simple, alternate to subopposite, 5–7 cells thick, often with secondary pinnae about 5 cells thick, truncate or hardly rounded at the apex. *Rhizoids* in restricted fields on ventral surface of main axes or bases of pinnae, hyaline to pale brown. *Monoecious*. *Male branches* uniformly very short to 1 mm long, with 1–6 pairs of antheridial chambers, singly or in pairs on one or both sides or remote on female branch. *Female branches* solitary, with or without small accessory basal branches. *Sporophytes* unknown in Antarctica.

Taxonomic and nomenclatural notes. — This species was described by Stephani (1905) as *Aneura georgiensis* from material collected on South Georgia by the Swedish South Polar Expedition of 1901–1903. It was transferred to *Riccardia* by G. Hässel de Menendez but there is some confusion regarding the effective publication of *R. georgiensis*. According to the *Index hepaticarum* (Geissler & Bischler, 1990) this combination was made in the revision of southern South American *Riccardia* (Hässel de Menendez, 1972). However, in fact this name was validly published a year ealier in the paper of Grolle (1971*c*) on liverworts of Îles Crozet. In this paper the final name is *Riccardia georgica*, not *R. georgiensis*, but this is evidently a misprint because the basionym is cited correctly.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In addition, Schuster (1989) described a separate subspecies (subsp. *sympodea* R. M. Schust.) from Marion Island, Prince Edward Islands in the Subantarctic, on the basis of differences in the gametangial characters, but also indicated the difference in the shape of the thallus in transverse section. He suggested that it is likely that this subspecies deserves recognition as a species in its own right if the difference in spatial arrangament of male and female gametangia proves constant. The material of this taxon is still very scanty, but one Antarctic population agrees perfectly in its characters with the plants from Marion Island as described and illustrated by Schuster (1989), and this supports the assumption that subsp. *sympodea* represents a separate species.

Differentiation. — *Riccardia georgiensis* is unlikely to be confused with any other local species of liverwort in Antarctica. It is easily known by its ribbon-like thalli which are convex dorsally in transverse section and flat or concave on the ventral surface. The segments of the main thallus have blunt, hardly to conspicuously and tumid margins. A characteristic feature of the species is a prominent ventral median band of large, elongated cells occupying 0.6–0.8 of the thallus width. Recognition of the infraspecific taxa within *R. georgiensis* is difficult, mostly due to the sterile condition of the plants. Of four specimens of this species known from the Antarctic only one, from Livingston Island (*Schulz 161*), has abundant gametangia, whereas the remaining specimens lack gametangia; unfortunately, these are the safest character for differentiating the two subspecies. The characters separating these subspecies are summarised in the following couplet:

1. Margins of the main thallus segment blunt but hardly rounded; ventral surface band of elongated cells bistratose, composed of cells almost identical in size to each other but much smaller than medullary cells and never conspicuously thick-walled, both often mycorrhizal; male branches to 1 mm long, linear, with 3–6 pairs of antheridial chambers, usually remote from female branches and never sympodial with them; female branches solitary, usually without small accessory basal branches . . . . subsp. ***georgiensis***

1. Margins the main thallus segment tumid and conspicuously rounded; ventral surface band of elongated cells unistratose, composed of very small and often thick-walled cells, not mycorrhizal; male branches very short, with 1–2 pairs of antheridial chambers, arranged singly or in pairs on one or both sides of female branch; female branches often with a narrow, short, simple sterile branch at base, on one or both sides . . . . subsp. ***sympodea***

The single specimen from Livingston Island (Fig. 85) agrees in all details of the gametangial characters with the plants recognised by Schuster (1989) as subsp. *sympodea*. The only difference is the lack of thick-walled, unistratose ventral

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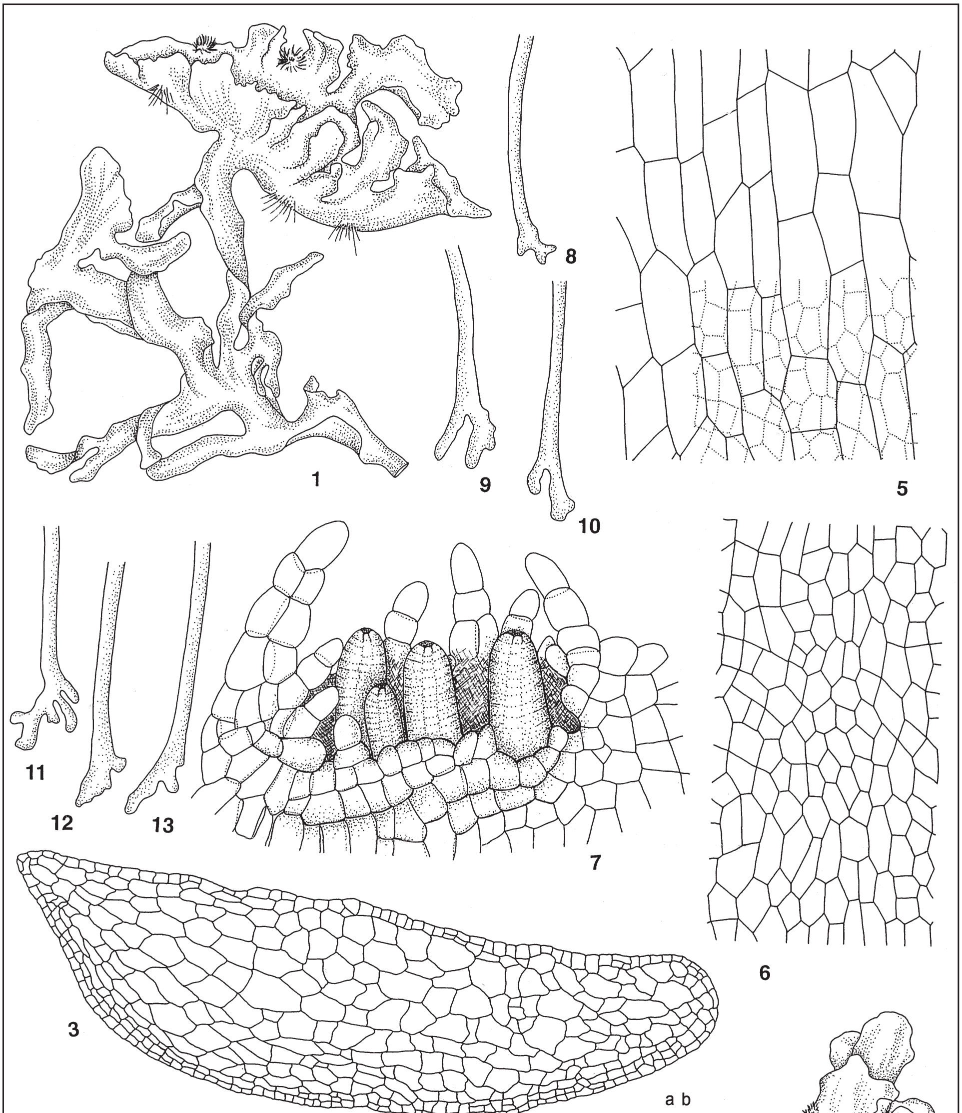
FIGURE 84. *Riccardia georgiensis* cf. subsp. *georgiensis*. **1–3**. Sterile plants. **4**. Portion of ultimate thallus segment, showing areolation. **5**. Portion primary branch, showing epidermal cells. **6–7**. Transverse sections in middle of ultimate segments. **8–9**. Transverse sections of primary branch. (All from *Longton 783b*, AAS.) Scale bars: a – 100 µm (4–9); b – 1 mm (1–3).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epidermis, but the thallus has conspicuously thickened and rounded margins. Conversely, the specimens from the South Sandwich Islands (Fig. 84) are entirely sterile and they have the main thallus segments with blunt but rather thinly rounded margins. Additionally, the ventral surface band is bistratose and composed of thin-walled cells. These two characters suggest subsp. *georgiensis*, but without the gametangial characters this cannot be confirmed.

Reproduction in Antarctica. — Fertile plants unknown but gametangia have been found in a single population.

Habitat. —On moist ash and fine scoria around fumarole vents, and amongst *Deschampsia antarctica*.

World range. — An amphiatlantic south-temperate species (Fig. 86), widely distributed in Tierra del Fuego, the Magellan Strait islands (Hässel de Menendez, 1972) and on the Brunswick Peninsula (Engel, 1978), extending northward to lat. *ca* 50°S in Chile and Argentina, the Falkland Islands (Engel, 1990*a*) and South Georgia (from where it was originally described; Stephani, 1905), and penetrating into the Antarctic botanical zone on the South Sandwich and South Shetland Islands. Additionally, it is known from the Prince Edward Islands (as subsp. *sympodea*) and Îles Crozet and in the Subantarctic. Engel (1978) considers *Riccardia georgiensis* to be subantarctic in distribution, but the species occurs frequently near sea level on the Falkland Islands (Engel, 1990*a*) and on the Brunswick Peninsula in southern South America (Engel, 1978), indicating that it should be considered as a temperate, rather than a subantarctic species. *R. georgiensis* has the same distribution pattern as *R. prehensilis* (Hook. f. & Taylor) C. Massal., which is considered by Engel (1978, 1990*a*) as an amphiatlantic south-temperate species.

Distribution in Antarctica. — Known only from two volcanic islands in the South Sandwich Islands archipelago (subsp. *georgiensis*), and Livingston Island in the South Shetland Islands (subsp. *sympodea*) (Fig. 87).

Specimens examined: **cf. subsp. *georgiensis*** — SOUTH SANDWICH ISLANDS. VISOKOI ISLAND. Finger Point, *ca* 35 m, *Longton 764* (AAS, KRAM). CANDLEMAS ISLAND. North of eastern lagoon, 50 m, *Longton 783B & 784* (AAS, KRAM).

subsp. *sympodea* — SOUTH SHETLAND ISLANDS. LIVINGSTON ISLAND. ***Hurd Peninsula***: South Bay, Johnson;s Dock, 5 m, *Schulz 161* (Hb. Schulz, KRAM).

Literature records. — SOUTH SANDWICH ISLANDS: without indication of the island (Lewis Smith, 1993: 322); Visokoi (Grolle, 1972*a*: 85; Hässel de Menendez, 1972: 128: Longton & Holdgate, 1979: 11; Ochyra & Váňa, 1989*b*: 218); Candlemas Island

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FIGURE 85. *Riccardia georgiensis* subsp. *sympodea*. **1–2**. Portions of plants, dorsal aspect. **3–4**. Transverse sections of main axis. **5**. Cells of median part of ventral epidermis. **6**. Dorsal epidermal cells. **7**. Gynoecium. **8–13**. Rhizoidal apices. (All from *Schulz 161*, KRAM.) Scale bars: a – 100 µm (3–13); b – 1 mm (1–2).

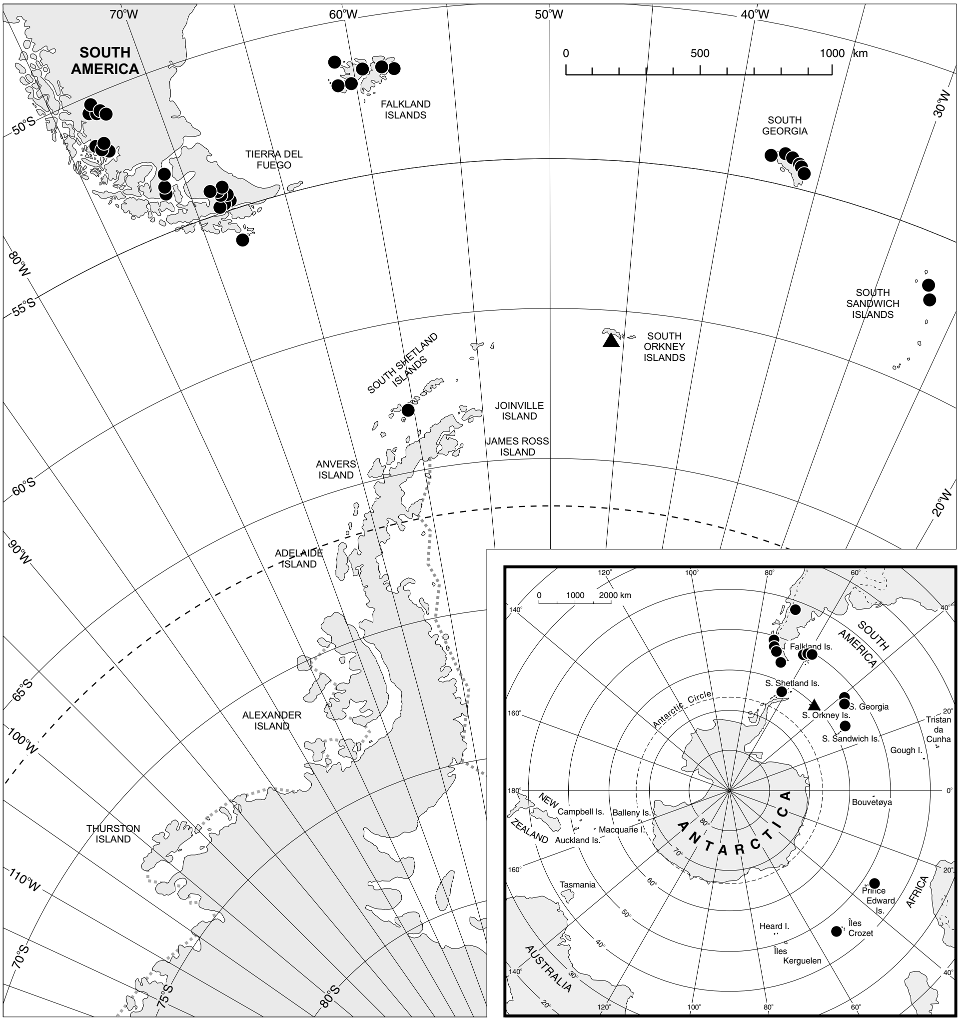

FIGURE 86. Distribution of *Riccardia georgiensis* in the Antarctic and Fuegian region. Inset: global distribution. The locality of an unnamed species of *Riccardia* on Signy Island is indicated by a triangle.

(Longton, 1966: 85; 1967: 228 both as *Riccardia* sp.; Grolle, 1972*a*: 85; Hässel de Menendez, 1972: 128: Longton & Holdgate, 1979: 11; Ochyra & Váňa, 1989*b*: 218). SOUTH SHETLAND ISLANDS: Livingston Island (Sancho *et al*., 1999: 322).

Note. — An indeterminable specimen of *Riccardia* (with only a single and not well differentiated thallus) was collected on Signy Island on the ridge north of Thulla Point at alt. 50 m (*Lewis Smith 500*, AAS) (Lewis Smith & Gimingham, 1976).

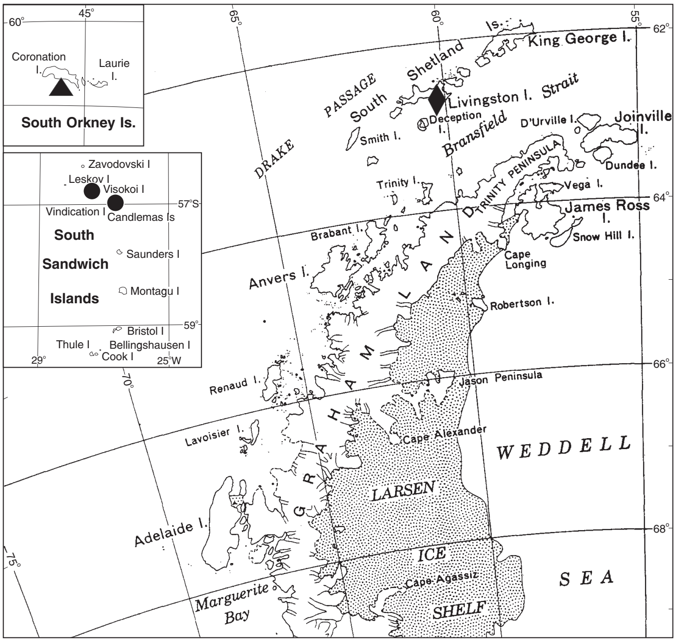

FIGURE 87. Distribution of *Riccardia georgiensis* subsp. *sympodea* (rhomb) and cf. subsp. *georgiensis* (dots) in the Antarctic. The locality of an unnamed species of *Riccardia* on Signy Island is indicated by a triangle.

Family **XI. METZGERIACEAE** H. KLINGGR.

Metzgeriaceae H. Klinggr., Höh. Crypt. Preuss.: 10. 1858. – TYPE: *Metzgeria* Raddi.

Plants thallose, prostrate or procumbent, in intricate mats, adhering to the substratum or rarely pendulous, simple or more commonly with terminal and ventral-intercalary branches, pale green or green, sometimes bluish in herbarium material. *Thalli* ligulate to linear, differentiated into a sharply-defined, multistratose costa, 5–8 cells high and constantly unistratose, delicate, lateral wings; wing cells thin-walled or weakly thick-walled, mostly 5–6-angled; elongate, setose, bristle-like hairs variously present on margins and surfaces of laminae. *Asexual reproduction* uncommon by gemmae or small branches. *Dioecious* or *autoecious*. *Male* and *female inflorescences* on ventral-intercalary branches *Male branches* often circinate, with incurved margins, antheridia in 2 rows along the dorsal face of costa. *Female branches* almost flat, obtuse to bilobed. *Shoot calyptra* fleshy, hairs present. *Seta* about 4–10 cells wide, epidermal cells in 12–32 rows. *Capsule* subglobose; capsule wall bistratose; outer wall with nodular, inner with semiannular thickenings. *Spores* small; elaters unispiral; elaterophores well developed; spore/elater width ratio 3–4(–5) : 1.

A cosmopolitan family widely distributed throughout the world, although rare in polar regions of both Hemispheres. About 240 species have been described in this group, but this number has been reduced to about 140 species as a result of taxonomic studies, for example in tropical Asia, Australasia and Pacific region (Kuwahara, 1966) and in the Neotropics (Kuwahara, 1986). However, Schuster (1992*a*) believed that a critical worldwide revision would probably reduce the number to less than 80 species. Kuwahara (1978), recognised five genera in this family four of which, *Apometzgeria*, *Apertithallus*, *Steereella* and *Austrometzgeria*, were segregates of the large genus *Metzgeria*. Only one of them, the curious monotypic genus *Austrometzgeria* from Australasia, was accepted by Schuster (1992*a*), whereas the others were given the status of subgenera within *Metzgeria*. This genus is represented in Antarctica by a single species.

1. METZGERIA RADDI

Metzgeria Raddi, Jungermanniografia Etrusca: 34. 1818. – LECTOTYPE: *Metzgeria glabra* Raddi, *nom. illeg.* = *Metzgeria furcata* (L.) Dumort. (*Jungermannia furcata* L.) (*fide* Kuwahara, 1966: 217).

Plants prostrate or procumbent in thin mats or ascending in weft-like mats, sometimes in pendent mats or in small compressed cushions, pale green, regularly pseudodichotomously or rarely pinnately branched. *Thalli* very narrow to narrow or seldom moderately wide, with a unistratose, never lobate lamina arising from a well defined costa; laminal cells hexagonal, thin-walled; costa with 2–4 rows of large, thin-walled epidermal cells on both surfaces surrounding 2–4-stratose, smaller, uniformly thickened medullary cells; hairs stiff, elongate, setose, straight or curved, variously scattered on margins or surfaces of laminae; oil-bodies absent or minute. *Rhizoids* scattered on ventral surface. *Gemmae* sometimes borne on wing margins or on modified branches. *Dioecious* or *autoecious*. *Male branches* dwarf, involute, hairless, with a costa. *Female branches* dwarf, involute, subglobose, strongly hairy, without costa. *Calyptra* pyriform, fleshy, hairy above. *Seta* 4–6 cells in diameter. *Capsule* dehiscing by 4 valves, spherical to short-ovoid. Spores weakly papillose or smooth; elaters long, attenuate, with a wide pale or yellow band.

A large and taxonomically difficult genus with nearly cosmopolitan distribution but with particular concentration of species in tropical regions. Kuwahara (1986) recognised 134 species in *Metzgeria* but the final number is probably much lower. One species is known from very scattered localities in the maritime Antarctic.

1. *Metzgeria decipiens* (C. MASSAL.) SCHIFFN. FIG. 88

Metzgeria decipiens (C. Massal.) Schiffn. *in* Engl., Forschungsr. Gazelle Bot. **4**: 43. 1890. – *M. furcata* (L.) Dumort. var. *decipiens* C. Massal., Nuov. Giorn. Bot. Ital. **17**: 256. 1885. – TYPE: Ad arborum truncos cum hep. alliis ex insula Statuum (Basil-Hall, port Vancouver); Febr.-Mart, c. fr. [HOLOTYPE: VER? (*non vidi*); ISOTYPE: YU (*non vidi*)].

Plants small, 1–2 cm long with branches 0.8–1.5 mm wide, prostrate or procumbent to suberect in compact shallow tufts, pale or yellowish-green. *Thalli* freely furcately branched, with ventral-intercalary branches, plane to slightly convex, 7–25 cells wide; wing cells thin-walled, without or with minute trigones, 15–25 × 20–40 µm on margins, 20–35(–40) × 30–50(–70) µm in the middle; costa in transverse section on both sides weakly arched, with epidermal cells in

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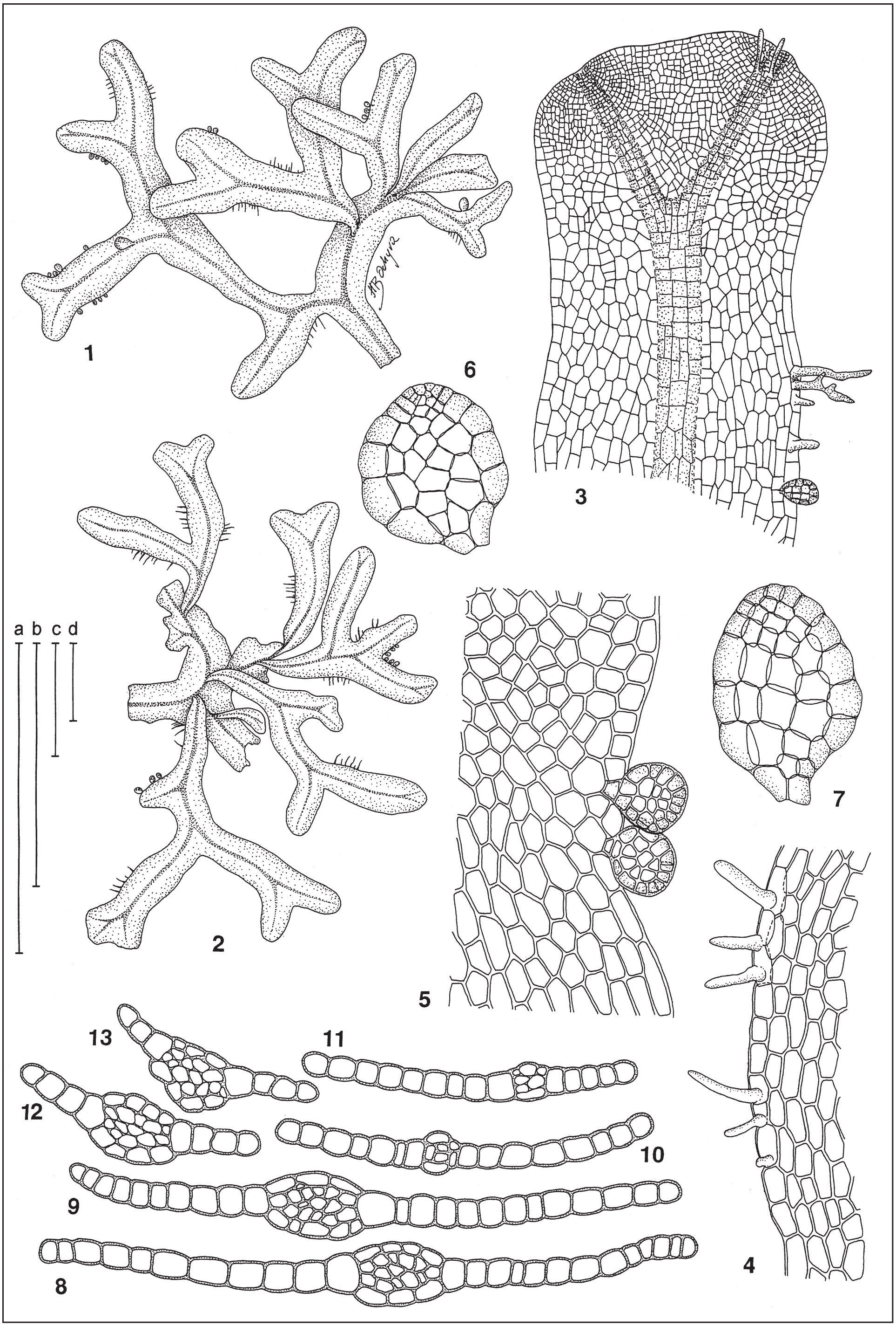
FIGURE 88. *Metzgeria decipiens*. **1–2**. Plants, dorsal aspect. **3**. Thallus apex, ventral aspect, showing slime papillae. **4**. Marginal part of thallus with marginal hairs. **5**. Thallus wing cells with gemmae. **6–7**. Gemma. **8–13**. Transverse section of main thallus. (All from *Corner 595*, AAS.) Scale bars: a – 5 mm (1–2); b – 0.5 mm (3); c – 100 µm (6–7); d – 100 µm (4–5, 8–13).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2 rows on both ventral and dorsal surfaces, 20–35 × 25–70 μm; medullary cells (8–15) in 2–4 tiers, occasionally reduced to only 1 cell; hairs sparse on the thallus margin and ventral surface of costa, occasionally absent. *Remainder* unknown.

Taxonomic and nomenclatural notes. — *Metzgeria decipiens* is close to *M. furcata* (L.) Dumort. from the Northern Hemisphere, and was originally described by Massalongo (1885) as a variety of this species. Schiffner (1889) raised it to the rank of a separate species and since then its status has not been changed. The species is very variable throughout its wide geographical range and a detailed taxonomic and phytogeographic account of this species was published by Kuwahara (1983).

Differentiation. — As the only species of this genus and family in the Antarctic with its characteristic appearance, *Metzgeria decipiens* cannot be confused with other regional liverwort species.

Reproduction in Antarctica. — Fertile plants unknown, but gemmae are produced abundantly.

Habitat. — In moist shaded rock crevices, on rock ledges associated with chasmophytic bryophytes e.g. *Didymodon brachyphyllus*, *Distichium capillaceum, Plagiothecium georgico-antarcticum* and *Pohlia cruda*.

World range. — *Metzgeria decipiens* is considered here as a pan-south-temperate species (see Kuwahara, 1983) rather than amphipacific-south-temperate species as designated by Engel (1978, 1990*a*), or circumsubantarctic as described by Grolle (1971*a*). It has its centre of occurrence in the *Nothofagus* zone of southern South America where it ranges from the Juan Fernandez Islands to Tierra del Fuego and the Falkland Islands. It is rarer in New Zealand, Tasmania, south-eastern Australia New Caledoania, Norfolk Island, but it is also known from South Africa extending to the subantarctic Prince Edward Islands (Grolle, 1971*a*) and Îles Kerguelen (Schiffner, 1889) in the South Indian Ocean. It is one of only a few austral species which extends northwards into the tropics, and even into the Himalayas and Japan in the Northern Hemisphere. It is widely distributed in the tropics, occurring exclusively at high elevations, e.g. in the northern Andes in South America and Central America, tropical Africa, Malesia, the Philippines and the Hawaiian Islands (Fig. 89).

Distribution in Antarctica. — A widely distributed but scattered and localised species known only from Signy Island in the South Orkney Islands and a few sites on the western coast of the Antarctic Peninsula, on the Danco and Graham Coasts, to the Berthelot Islands at lat. 65°20'S. It is a species of lower elevations, occurring from near sea level to about 85 m (Fig. 90).

Specimens examined. — SOUTH ORKNEY ISLANDS. SIGNY ISLAND. East-west ridge between North Point and coast opposite Spindrift Rocks, *ca* 85 m, *Longton 1138* (AAS, KRAM); south-east shore of Factory Cove, 10–15 m, *Longton 838* (AAS, KRAM); Factory

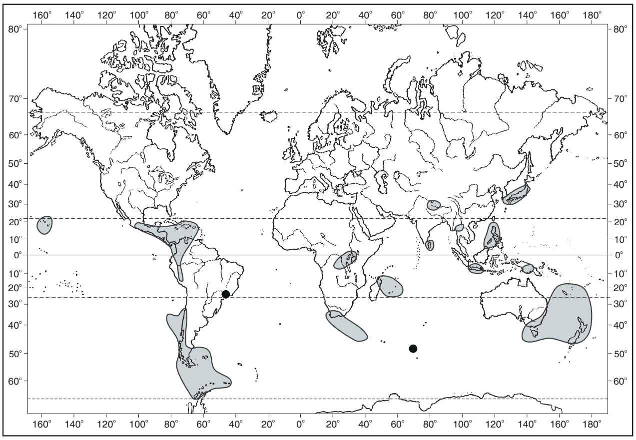

FIGURE 89. Global distribution of *Metzgeria decipiens*.

Bluffs, 35 m, *Lewis Smith 1843 & 5228* (AAS, KRAM); north side of Observation Bluff, *ca* 85 m, *Lewis Smith 11* (AAS, KRAM); east side of Rusty Bluff above Paal Harbour, 80 m, *Lewis Smith 5194* (AAS, KRAM) and *ca* 85 m, *Lewis Smith 463* (AAS, KRAM); cliffs above Paal Harbour, *Lewis Smith 8220* (AAS, KRAM).

WEST ANTARCTIC PENINSULA. **Danco Coast**. Cierva Point, *Komárková 589* (KRAM). **Graham Coast**. Cape Tuxen, *ca* 15 m, *Corner 672B* (AAS, KRAM). ***Petermann Island***: north coast, *ca* 13 m, *Corner 720* (AAS, KRAM), *ca* 15 m, *Longton 1343B* (AAS, KRAM) and 27 m, *Corner 805* (AAS, KRAM). ***Argentine Islands***: north-east of Uruguay Island, *ca* 6 m, *Corner 595* (AAS, KRAM) and *ca* 15 m, *Corner 717B* (AAS, KRAM);

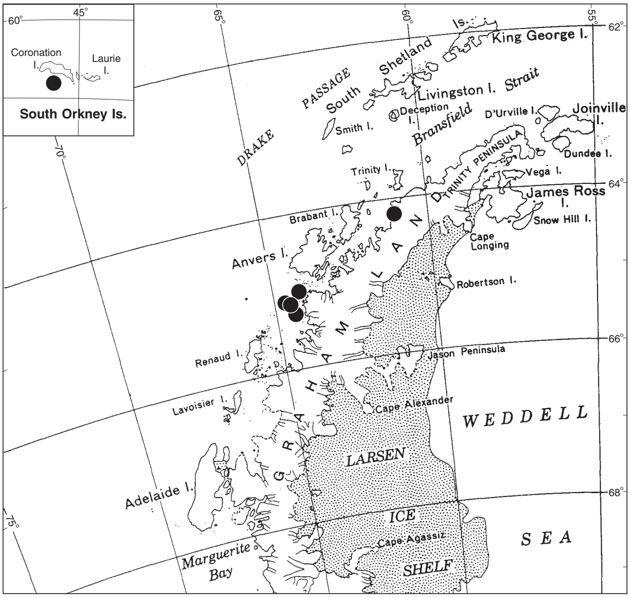

FIGURE 90. Distribution of *Metzgeria decipiens* in the Antarctic.

north coast of Uruguay Island, *ca* 35 m, *Longton 1374* (AAS, KRAM); Skua Island, *ca* 8 m, *Longton 1334* (AAS, KRAM); Irizar Island, *ca* 6 m, *Corner 604B* (AAS, KRAM). ***Berthelot Islands***: north side of the largest island, *ca* 35 m, *Corner 629* (AAS, KRAM).

Literature records. — SOUTH ORKNEY ISLANDS: Signy Island (Longton, 1966: 85; Lewis Smith, 1972: 19, 28; 1996*a*: 31, 33; Ochyra & Váňa, 1989*b*: 219 all as *Metzgeria* sp.). WEST ANTARCTIC PENINSULA: Graham Coast (Lewis Smith & Corner, 1973: 115–116; Ochyra & Váňa, 1989*b*: 219 both as *Metzgeria* sp.; Lewis Smith, 1996*a*: 31, 33).

Order III. MARCHANTIALES LIMPR.

Marchantiales Limpr., Kryptogamen-Fl. Schlesien **1**: 239, 336. 1877 ["Ordn. Marchantiaceae"]. – TYPE: *Marchantia* L. emend. Raddi.

Plants thalloid, small to very large, in loose or crowded patches or scattered, prostrate, simple or dichotomously branched, with ventral or rarely lateral innovations. *Thalli* differentiated into a unistratose or rarely bistratose dorsal epidermis, mostly with air pores, and photosynthetic tissue formed of air chambers and compact parenchymatic basal tissue. *Rhizoids* of two types: one smooth-walled, the other with tuberculate thickenings projecting into cell lumen. *Asexual reproduction* usually lacking or occasionally by means of discoid gemmae borne in dorsal cupules or ventral bulbils, tubers or stolons. *Monoecious*, *dioecious*, *autoecious* or *paroecious*. *Antheridia* scattered or in groups sunken in the thallus, sessile on the thallus or on stalked receptacles. *Archegonia* in groups, either apical, or more commonly elevated on archegoniophores. *Sporophyte* differentiated into bulbous foot, short seta and capsule, or undifferentiated (only capsule). *Capsule* dehiscing by several valves or opening by operculum or desintegration of capsule wall. *Spores* large, mostly polar, variously sculptured; elaters usually 2–3-spiral, rarely reduced or absent.

The Marchantiales are considered to be one of the peaks of liverwort evolution (Schuster, 1984). They exhibit a markedly complex tissue differentiation in the gametophyte and extreme sporophyte reduction (in the Riccineae). Members of this order have a worldwide distribution from the High Arctic to the Antarctic and many of them are pioneers of harsh environments in semi-arid and arid areas. Some of them are also colonisers of disturbed habitats. The order consists of about 380 species, 150 of which belong to *Riccia*, 80 to *Asterella* and 36 to *Marchantia*. They are classified into five suborders, 14 families and 28 genera. An excellent review of the taxonomic and evolutionary problems of this order was provided by Bischler (1998). In the Antarctic one (possibly two) species of the cosmopolitan genus *Marchantia* have so far been encountered.

Family XII. MARCHANTIACEAE (BISCHOFF) ENDL.

Gen. Pl.: 44. 1836 ["Ordo Marchantiaceae"]. – Trib. Marchantieae Bischoff, Nova Acta Leop.-Carol. **17**(2): 931, 969. 1835. – TYPE: *Marchantia* L. emend. Raddi.

Plants medium sized to large and robust, in crowded mats, green to dark green, sometimes leathery, rarely translucent. *Thalli* dorsally flat, margins lobulate, crenulate or undulate, occasionally sparsely hirsute, dichotomously furcate; branches broadly band-shaped or narrowly ribbon-shaped, notched at the apex; dorsal epidermis mostly unistratose with thin- to moderately thicker-walled cells lacking trigones and chloroplasts, areolate because of compound, barrel-shaped pores formed of several superimposed concentric rings of cells; air-chamber in the assimilatory tissue present, occasionally reduced or absent, usually densely packed with 2–5-celled chlorophyllose filaments, occasionally lacking or reduced; parenchymatic tissue in the ventral part of thallus or occupying almost all of it, compact, sometimes with a few sclerotic cells. *Ventral scales* in 2–6 rows, the largest scales lunate with appendages. *Rhizoids* polymorphic, the narrower with strong internal thickenings, the widest with few or no internal pegs or thickenings. *Asexual reproduction* frequent by discoid gemmae borne in dorsal, hollow, cup-shaped cupules. *Monoecious* or *dioecious*. *Antheridiophores* with a very short to fairly long stalk with 2 rhizoidal grooves; receptacles discoid, lobed, rayed or undivided; antheridia sunken in dorsal side. *Archegoniophores* on very long, 2-furrowed stalk; receptacles obscurely to distinctly lobed. *Capsules* ovoid to subglobose, dehiscing by irregular slits from the apex downwards; capsule wall unistratose with annular to semiannular thickenings. *Spores* small, ± triangular-globular, variously ornamented but not reticulate; elaters slender, tapering at ends, 2–3-spiral; spore/elater width ratio more than 4 : 1.

A medium-sized family subdivided by Schuster (1992*b*) into three subfamilies, Marchantioideae, Bucegioideae and Dumortieroideae. In total, it comprises about 40 species and five genera (Bischler, 1998). Four of these are monotypic genera, namely the Holarctic *Preissia* Corda and *Bucegia* Radian, subantarctic *Neohodgsonia* H. Perss. and cosmopolitan *Dumortiera* Nees, whereas the largest genus *Marchantia* consists of 36 species distributed worldwide. Only the latter genus is known in the Antarctic.

1. MARCHANTIA L. emend. Raddi

Marchantia L., Sp. Pl.: 1137. 1753. – LECTOTYPE: *Marchantia polymorpha* L. emend. Raddi (*fide* Knowlton, 1894: 459; Evans, 1917: 205).

Plants thallose, medium-sized to large and robust, perennial, prostrate or sometimes ascending, in moist habitats, green to dark green, often tinged with purple, especially at margins, drought-tolerant. *Thalli* wide to very wide, 2.7–20.0 mm wide, dichotomously to monopodially branched, with branches obcordate to linear, notched at the apex, margins lobulate, crenulate to undulate, hairless; dorsal epidermis 1(–2)-layered, areolate with elevated, compound pores consisting of 4–7 concentric rings of cells with inner ring of collapsed cells; air-chambers in a single layer, with chlorophyllose, 2–5-celled filaments with the uppermost cells in contact with epidermis; ventral tissue compact, 2–3-layered at margins, parenchymatous, with oil-cells and often with sclerotic cells, mucilage cavities and pitted cell walls. *Ventral scales* arcuate or obliquely inserted in 4–10 rows with distal row extending to thallus margin or slightly exceeding it, with oil-cells and marginal papillae, each pair of different shape, 2 median rows with large appendage. *Rhizoids* smooth or pegged. *Gemmae* present, discoid, borne in dorsal cupulate receptacles with lobed-laciniate or dentate margins. *Dioecious*. *Antheridial receptacles* peltate or palmate, 2–12-lobed with compound, barrel-shaped pores on the dorsal side and scales underneath, exserted on short, nearly circular stalks, with 2–4 rhizoid furrows and 1–2 bands of green assimilatory tissue. *Archegonial receptacles* deeply 2–13-lobed, with compound pores on the dorsal face and archegonial cavities on the ventral surface, each with up to 14 archegonia and without paraphyses, exserted on long stalks with 1–2 rhizoid grooves and 1–2 assimilatory strips. *Involucres* laterally compressed, truncate and bilabiate with lobed fimbriate margins; pseudoperianth delicate, membranous-campanulate contracted to tubular and plicate mouth. *Sporophytes* several per involucre, with cup-shaped foot and short seta; capsule subspherical, dehiscing by irregular slits. *Spores* small, thin-walled, ± triangular-globular, ornamented with thin, irregularly convoluted ridges or with wide ridges and granules between; elaters 2–3-spiral.

A medium-sized genus comprising some 36 species distributed worldwide. Bischler (1984, 1989, 1993) presented three monographs of *Marchantia* comprising, respectively, the neotropical, Asiatic and Pacific as well as European and African species. Two species have been reported from the Antarctic region, but no voucher collections of *M. polymorpha* have been available for examination.

KEY TO THE ANTARCTIC SPECIES OF *MARCHANTIA*

1. Thalli with lobulate margins, dorsally without dark median band; pores cruciate; cells bordering inner opening of epidermal pores with strongly convex inner walls; ventral scales in 4(–6) rows, not extending beyond thallus margins; median scale appendage large, margins entire or slightly crenulate, bordered with very small marginal cells .... **1. *M. berteroana***
1. Thallus margins entire or crenulate, dorsally often with dark median band; pores not cruciate; cells bordering inner opening of epidermal pores with slightly convex inner walls; ventral scales in 6 rows, extending beyond thallus margins; median scale appendage small, margins bordered with somewhat smaller marginal cells .... **2. *M. polymorpha***

1. ***Marchantia berteroana*** LEHM. & LINDENB. FIG. 91

Marchantia berteroana Lehm. & Lindenb. *in* Lehm., Nov. Stirp. Pug. **6**: 21. 1834. – TYPE: In insula Juan Fernandez legit cl. Bertero (Herb. Hookeri) [LECTOTYPE (*fide* Bischler, 1984: 44): W (*non vidi*); ISOTYPES: FH, G, NY, PC, STR, W (*non vidi*)].

Plants medium-sized to large, prostrate in rosettes coalescing into loose or intricate mats to erect open tufts, dull to shiny, green, yellowish- to bluish-green, often tinged with purple or brown. *Thalli* leathery, without distinct median band on the dorsal surface, not canaliculate, 3–5 cm long, 0.6–1 cm wide, dichotomously branched, branches irregularly furcate, with terminal segments broadly oblong, notched at the apex; margins crisped and irregularly lobulate, entire or minutely crenulate, hyaline, purplish or brown; dorsal epidermal cells unistratose, thin-walled, 40–60 × 15–35 μm; epidermal pores barrel-shaped, 45–70 μm in diameter, bordered by 4–7 rings of cells, 1–3 above epidermis, 2–4 projecting into air-chambers; the uppermost ring of 4–5 cells, the innermost cruciate because of the strongly protuberant inner cell walls, leaving only

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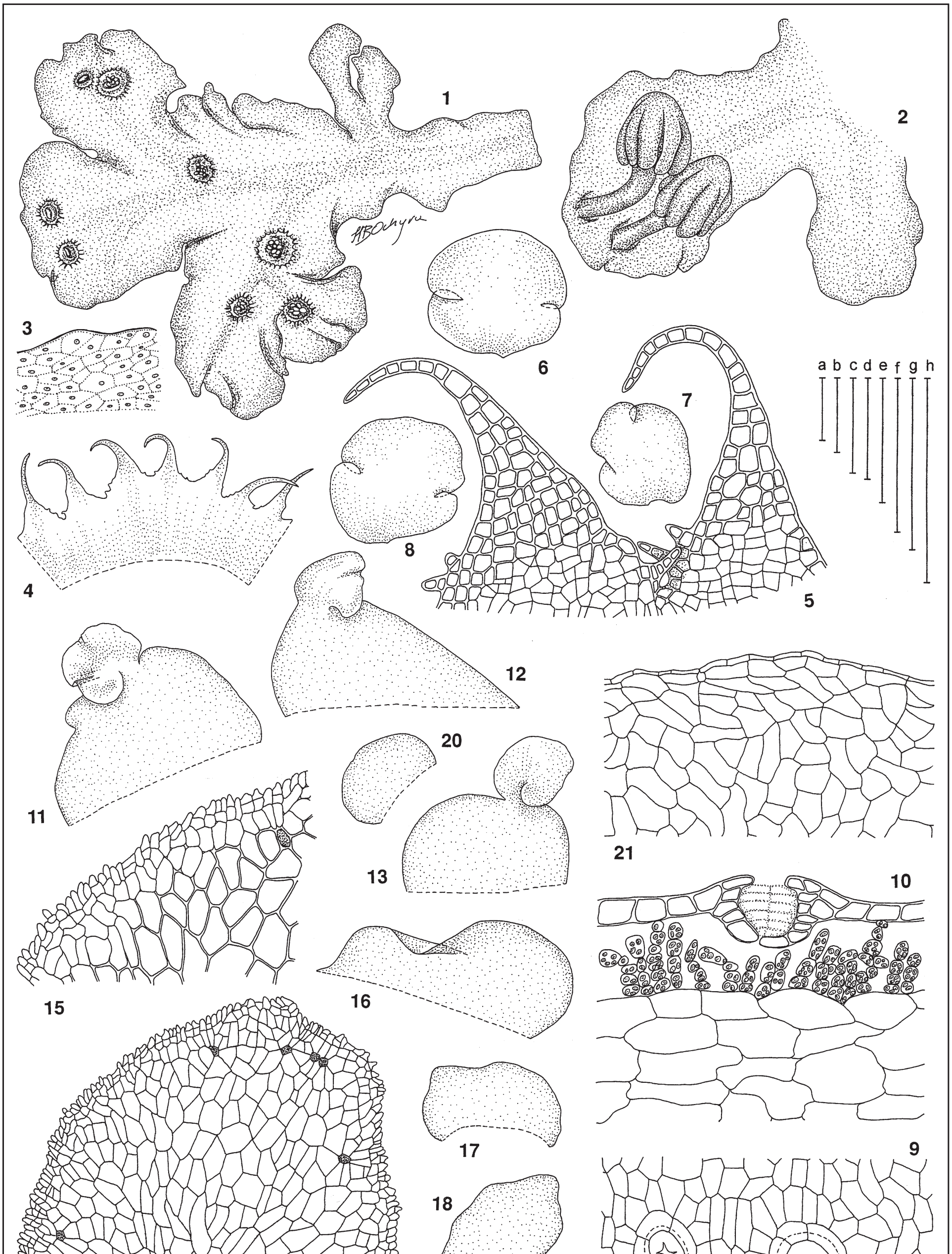
FIGURE 91. *Marchantia berteroana*. **1**. Sterile plant. **2**. Portion of female plant. **3**. Portion of thallus, showing areolation and pores. **4**. Lobes of a cupule. **5**. Two lobes of a cupule, external aspect. **6–8**. Gemmae. **9**. Two epidermal pores, external aspect. **10**. Transverse section of wing portion of thallus, showing aerenchyma-chlorenchyma layer with pore. **11–13**. Ventral scales with appendages. **14**. Areolation of appendage. **15**. Portion of upper margin of appendage. **16–20**. Ventral scales without appendages from lateral two rows. **21**. Areolation of upper part of ventral scale from lateral row. (1, 6–8 from *Newsham & Bucktrent 175A*; 2 from *Convey 246A*; 3–5 from *Convey 245K*; 9–21 from *Convey 222A*; all in AAS.) Scale bars: a – 1 mm (3) and 100 μm (5, 15); b – 1 mm (11–13, 16–20); c – 100 μm (9–10); d – 10 mm (2); e – 1 mm (4) and 100 μm (21); f – 1 mm (6–8); g – 5 mm (1); h – 0.5 mm (14).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a small opening; ventral tissue reaching 25 layers in the median portion of thallus. *Ventral scales* hyaline to purplish, cordate, rounded, with appendages; margins entire or slightly crenulate, bordered by small, subquadrate cells 10–25 × 10–20 µm; laminal scales wider than long, with rounded apex; marginal scales numerous to absent, ovate. *Gemmae* discoid, in crenulate cups scattered over the dorsal surface of the thalli. *Dioecious*. *Archegoniophores* at apex of main thallus; stalk to 20 mm long, with single, broad band of air-cavities and 2 rhizoid furrows; scales at base of stalk oblong or ovate, without appendage, apex rounded, brownish or hyaline; receptacle 6–8 mm in diameter, deeply dissected into 8–10 terete rays without papillae, nearly symmetric or slightly asymmetric, with basal sinus up to 80° wide. Involucre only about half of the ray length, hyaline or purplish at margin, with ciliate lobes. Only female plants known in the Antarctic.

Taxonomic and nomenclatural notes. — *Marchantia berteroana* was one of the earliest species in the genus to be described, based on specimens collected by C. G. Bertero on Juan Fernandez Islands (Lehmann, 1834). The species is very variable throughout its wide geographical range, and consequently it was described several times under different names. Bischler (1984, 1989, 1993) recognised 14 heterotypic synonyms of *M. berteroana*, and discussed its variability, taxonomy and ecology in some detail.

Differentiation. — The species is easily distinguished by the broad strap-like thallus, tiny marginal cells of the median scale appendages, cruciate dorsal pores and lobulate thallus margin. It may be confused with *Marchantia polymorpha*, but this species is readily separated from *M. berteroana* by its non-lobulate thallus margins and the marginal scales extending beyond the thallus margin. Additionally, *M. polymorpha* has the appendages of the median scales bordered with only somewhat smaller cells in contrast to the very small marginal cells in *M. berteroana.*

Reproduction in Antarctica. — Fertile plants unknown, but female plants with archegoniophores have been recorded on heated ground in the South Sandwich Islands. However, discoid gemmae are frequently produced in cupulate cups.

Habitat. — On moist or wet soil (usually mildly alkaline), gravel and rocks, on moist cliff ledges, ash, cinders and volcanic debris, on heated ground near fumaroles; also on mosses and soil along stream margins and amongst *Deschampsia antarctica*.

World range. — A pan-south-temperate species, widely distributed and frequently common and abundant in southern South America, on all subantarctic islands, in southern Africa including the Tristan da Cunha/Gough group, southern Australia and New Zealand, extending into the tropics in the northern Andes of Colombia and Venezuela, Galapagos Islands, Costa Rica, New Caledonia, New Guinea and Java in the Malesian region. Additionally, known from south-east Brazil and two mid-Atlantic islands, Ascension and St. Helena (Fig. 92, inset). For detailed distributions in particular regions the monographs of Bischler (1984, 1989, 1993), as well as local treatments for southern South America (Hässel de

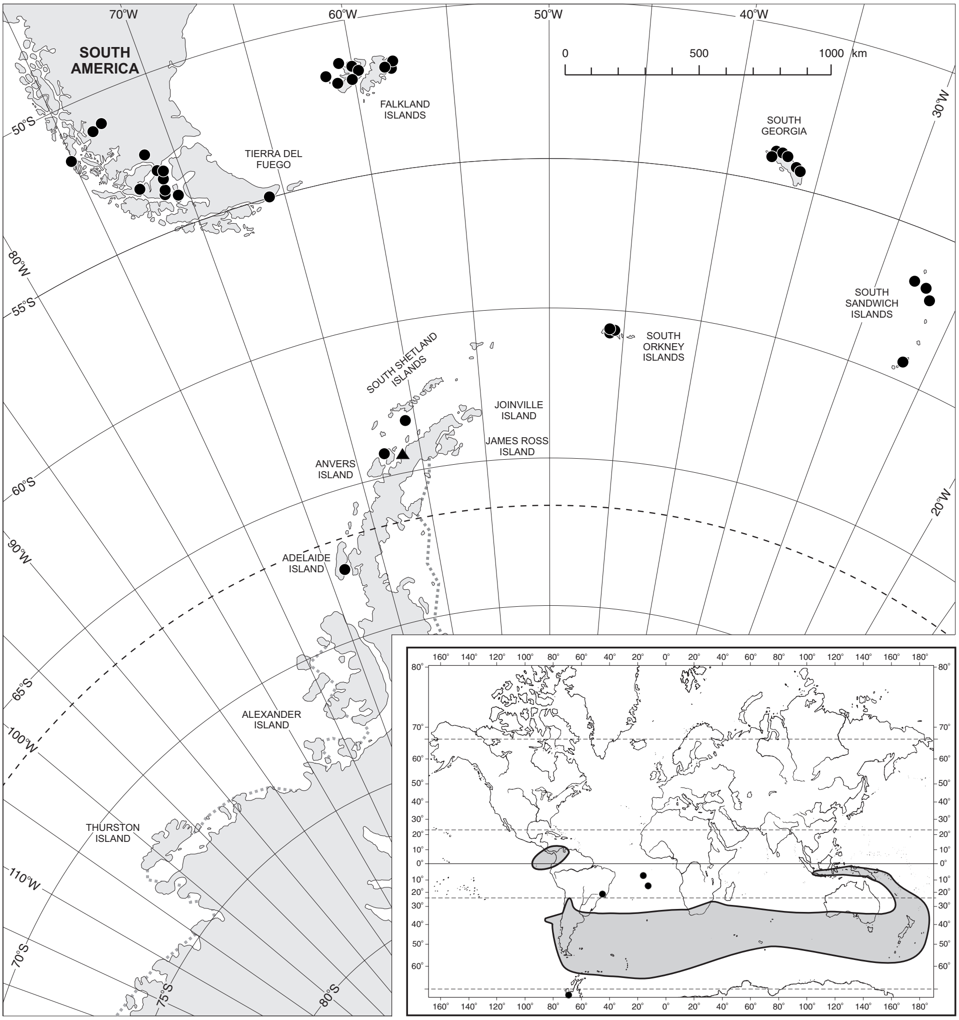


FIGURE 92. Distribution of *Marchantia berteroana* in the Antarctic and Fuegian region. Inset: global distribution. The literature report by Corte (1962) on the Danco Coast is indicated by a triangle.

Menendez, 1962; Engel, 1978), the Falkland Islands (Engel, 1990*a*) and southern Africa (Perold, 1995, 1999), should be consulted.

Distribution in Antarctica. — Widely distributed though localised throughout the northern maritime Antarctic (Fig. 93). It is particularly frequent on some volcanic islands in the South Sandwich Islands archipelago and occurs at several sites on Deception Island in the South Shetland Islands. Additionally, it is rather frequent on Signy Island, South Orkney Islands, and extends to lat. 67°36’S on Léo-

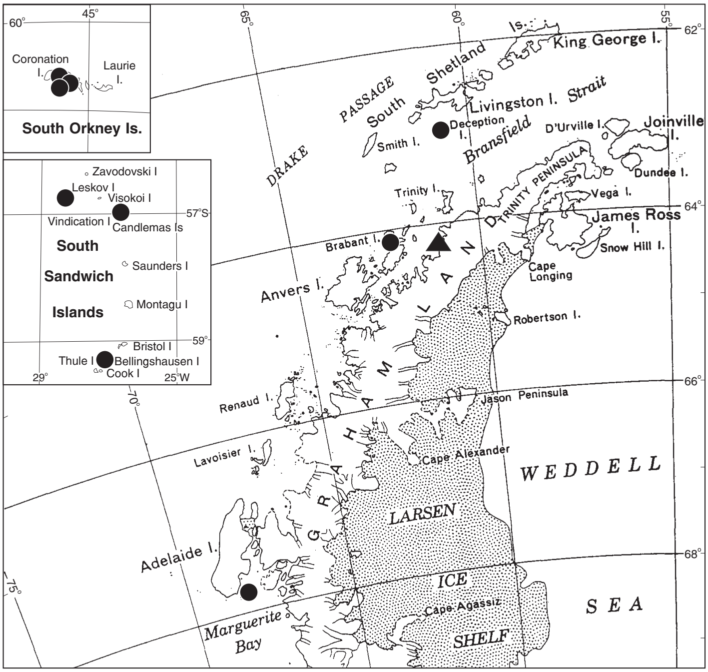


FIGURE 93. Distribution of *Marchantia berteroana* in the Antarctic. The literature report by Corte (1962) on the Danco Coast is indicated by a triangle.

nie Island on the Loubet Coast off the south-west Antarctic Peninsula. The species was first reported from Cabo Primavera on the Danco Coast (Corte, 1962), but unfortunately no specimens were available during the present studies.

Specimens examined. — SOUTH SANDWICH ISLANDS. **LESKOV ISLAND**. Summit ridge, 200 m, *Longton 485A & 498A* (AAS, KRAM). **VISOKOI ISLAND.** Summit ridge, *ca* 100 m, *Convey 245K & 246A* (AAS, KRAM); east side of summit ridge, ca 100 m, *Convey 247C, 249E & 251B* (AAS, KRAM). **CANDLEMAS ISLAND**. North-west ridge of Lucifer Hill, *Convey 175A* (AAS, KRAM); north-west fissure on Lucifer Hill, *Convey 222A* (AAS, KRAM); Lucifer Hill, north crater, *Convey 119E* (AAS, KRAM); Lucifer Hill, south edge of shallow gully above Clinker Gulch, *Convey 134B & 143C* (AAS, KRAM); Clinker Gulch, *Convey 156C & 159A* (AAS, KRAM); Lucifer Hill, base of north-west ridge, *Convey 230C* (AAS, KRAM); Lucifer Hill, north-west ridge active fissure, *Convey 232A* (AAS, KRAM); north of eastern lagoon, *Longton 786 & 790* (AAS, KRAM). **BELLINGSHAUSEN ISLAND.** South slope of cone, *ca* 75 m, *Holdgate 815B, 821A & 827A* (AAS, KRAM); south slopes of main cone (fumarole 1), *ca* 100 m, *Holdgate 411A & 419A* (AAS, KRAM) and *Convey 25B* (AAS, KRAM); crater rim west of access point, *ca* 170 m, *Convey 32F & 42D* (AAS, KRAM); inner south slope of crater, *Convey 63A & 64B* (AAS, KRAM); vents at floor of crater, 50 m, *Convey 71C* (AAS, KRAM); vents east of access point, 150 m, *Convey 72C* (AAS, KRAM); within crater, south-east rim, *Holdgate 824C* (AAS, KRAM).

SOUTH ORKNEY ISLANDS. **CORONATION ISLAND**. Shingle Cove, *ca* 65 m, *Lewis Smith 456* (AAS, KRAM); Cape Vik, 100 m, *Lewis Smith 565* (AAS, KRAM); north-east part of the island opposite Saunders Point, *ca* 6 m, *Lewis Smith 35B* (AAS, KRAM).

LYNCH ISLAND. Terrace on north side, 8–10 m, *Lewis Smith 533* (AAS, KRAM) and 20 m, *Lewis Smith 5182* (AAS, KRAM); without closer locality, *Lindsay 965A* (AAS, KRAM). **SIGNY ISLAND**. Between North Point and Robin Peak, *Lewis Smith 1840* (AAS, KRAM); west side of Jane Peak, 200 m, *Lewis Smith 462* (AAS, KRAM); south-east side of Factory Cove, 3 m, *Lewis Smith 5218* (AAS, KRAM). **MOE ISLAND**. Above Landing Cove, 5–50 m, *Lewis Smith 5239* (AAS, KRAM).

SOUTH SHETLAND ISLANDS. **DECEPTION ISLAND**. Entrance Point, 100 m, *Mason 47A* (AAS, KRAM); between Collins and Entrance Points, 50 m, *Lewis Smith 5770A* (AAS) and 60–80 m, *Lewis Smith 6730* (AAS, KRAM); Pendulum Cove, 50 m, *Lewis Smith 3645* (AAS, KRAM).

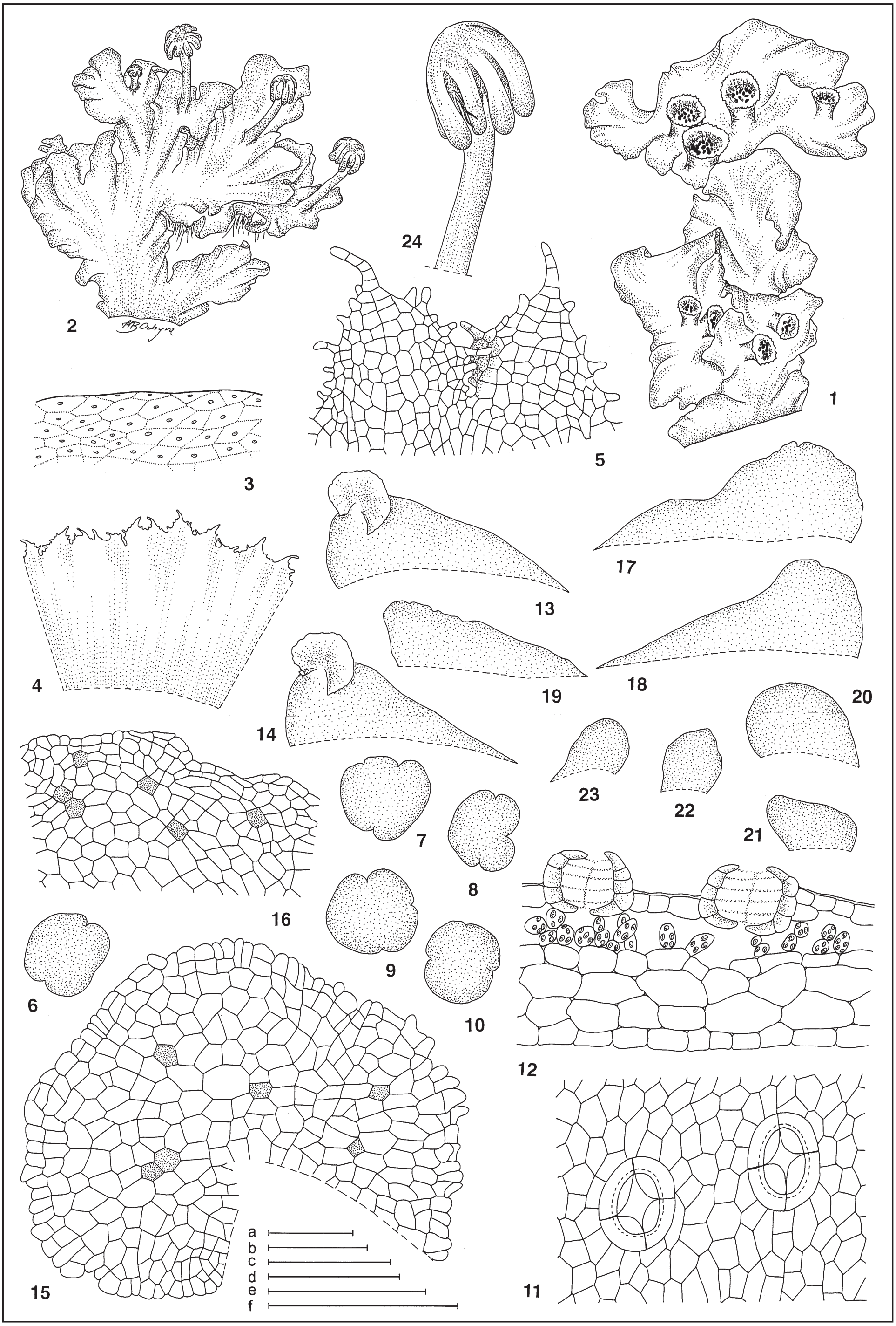
WEST ANTARCTIC PENINSULA. **DANCO COAST**. ***Palmer Archipelago***: Brabant Island, Claude Point, 200 m, *Hankinson 206C & 207A* (AAS, KRAM). **LOUBET COAST**. Léonie Island, 12 m, *Lewis Smith 9119* (AAS, KRAM).

Literature records. — SOUTH SANDWICH ISLANDS: Leskov and Bellingshausen Islands (Grolle, 1972*a*: 85; Gimingham & Lewis Smith, 1970: 767; Longton & Holdgate, 1979: 11; Ochyra & Váňa, 1989*b*: 219); Candlemans Island (Longton, 1967: 229 as *Marchantia* sp.; Grolle, 1972*a*: 85; Gimingham & Lewis Smith, 1970: 767; Longton & Holdgate, 1979: 11; Ochyra & Váňa, 1989*b*: 219). SOUTH ORKNEY ISLANDS: Lynch Island (Bonner & Lewis Smith, 1985: 82; Ochyra & Váňa, 1989*b*: 219); Signy Island (Longton, 1967: 219; Gimingham & Lewis Smith, 1970: 767; Lewis Smith, 1972: 30, 33, 37, 54, 62; 1993: 63; Lewis Smith & Gimingham, 1976: 36; Bonner & Lewis Smith, 1985: 77; Lewis Smith & Coupar 1986: 194); Ochyra & Váňa, 1989*b*: 219; Davey, 1997*a*: 220; 1997*b*: 189; 1997*c*: 26); Moe Island (Bonner & Lewis Smith, 1985: 68). SOUTH SHETLAND ISLANDS: Deception Island (Lewis Smith, 1984*b*: 56; 1984*c*: 29, 41, 43–44, 48; 1988*d*: 134; Ochyra and Váňa, 1989*b*: 219). WEST ANTARCTIC PENINSULA: Danco Coast (Corte, 1962: 5, 7; Ochyra & Váňa, 1989*b*: 219; Lewis Smith, 1996*a*: 31, 33–34).

2. ***Marchantia polymorpha*** L. emend. Raddi FIG. 94

Marchantia polymorpha L. emend. Raddi, Sp. Pl.: 1137. 1753. – TYPE: Dillenius, Hist. Musc. tab. 76 f. 6E–F, 1741 [LECTOTYPE; TYPOTYPE (*fide* Bischler & Boisselier-Dubayle, 1991: 363): OXF (*non vidi*)].

Plants large and robust, in crowded patches, bright, yellowish or dark green, dull, sometimes tinged with light red or brown. *Thalli* prostrate or ascending, to 5 cm long, 5–15 mm wide, with dark median line interrupted or indistinct or absent, dichotomously branched, with ultimate branches to 10 mm wide, faintly reticulate, with pores, margins plane to somewhat crisped; dorsal epidermal cells unistratose, thin-walled, without trigones, 30–50 × 20–25 μm; epidermal pores 50–85 μm in diameter, bordered by 4–6 rings of cells, 2–3 above epidermis, 2–3 projecting into air-chambers; cells bordering inner opening protruding into cavity, leaving large, not cruciate opening. *Ventral scales* in 6 rows, entirely covering ventral face and extending beyond thallus margins; median scale hyaline, rarely light red, obliquely triangular, narrowed above and constricted at meeting point with appendages; appendages rounded, brown or purple, margins denticulate, crenulate or entire, bordered by only slightly smaller cells; laminal scales wedge-shaped, much wider than long, hyaline or pale mauve, rounded at the apex, papillate on margins; marginal scales usually projecting beyond thallus margins, oblong or ovate, hyaline to brownish. *Gemmae* lenticular borne in cupules scattered over the dorsal surface of the thalli. *Dioecious*. *Male receptacles* apical, peltate, shallowly 8–10-lobed on stalks 2–3 cm high. *Archegoniophores* arising from the apex of terminal segment or main or short lateral branch, raised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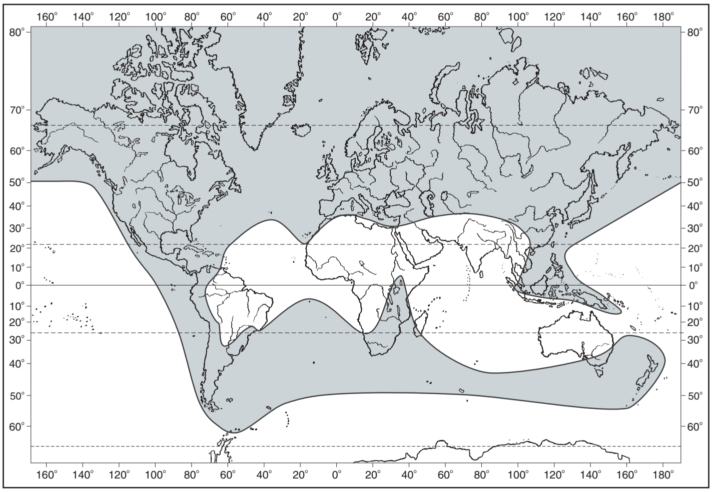

FIGURE 95. Global distribution of *Marchantia polymorpha*.

on stalk, 2–5 cm long; receptacle 6–8 mm in diameter, deeply dissected into 9–11 terete rays with numerous papillae. Involucre only about half of the ray length, hyaline or purplish at margin, with ciliate lobes. *Spores* 10–12 µm in diameter.

Taxonomic and nomenclatural notes. — *Marchantia polymorpha* was one of the first liverworts to be described and illustrated. The species was formally described by Linnaeus (1753) who was the first to note the protean nature of this species and recognised within it three varieties. *M. polymorpha* was lectotypified by Bischler and Boisselier-Dubayle (1991) and they recognised three subspecies within this highly polymorphic species.

Differentiation. — For differences with *Marchantia berteroana* see comment under this species.

Reproduction in Antarctica. — According to Young and Kläy (1971) no reproductive structures were observed.

Habitat. — On moist warm volcanic ash, cinders and debris.

World range. — *Marchantia polymorpha* is generally considered as a cosmopolitan species. It is widely distributed in cool and temperate regions in both Hem-

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FIGURE 94. *Marchantia polymorpha*. **1**. Dorsal face of sterile thallus with cupules. **2**. Portion of female plant. **3**. Portion of thallus, showing areolation and pores. **4**. Lobes of a cupule. **5**. Two lobes of a cupule, external aspect. **6–10**. Gemmae. **11**. Two epidermal pores, external aspect. **12**. Transverse section of wing portion of thallus, showing aerenchyma-chlorenchyma layer with pore. **13–14**. Ventral scales with appendages. **15**. Areolation of appendage. **16**. Portion of upper margin of appendage. **17–23**. Ventral scales without appendages from lateral two rows. **24**. Female receptacle. (1, 4–10 from *Greene 2982*; 2–3, 11–24 from *Greene 1600*; all in AAS.) Scale bars: a – 1 mm (3); b – 1 cn (1–2; c – 1 mm (4, 13–23), 200 µm (5, 16) and 100 µm (11); d – 100 µm (12); e – 1 mm (6–10) and 200 µm (15); f – 5 mm (24).

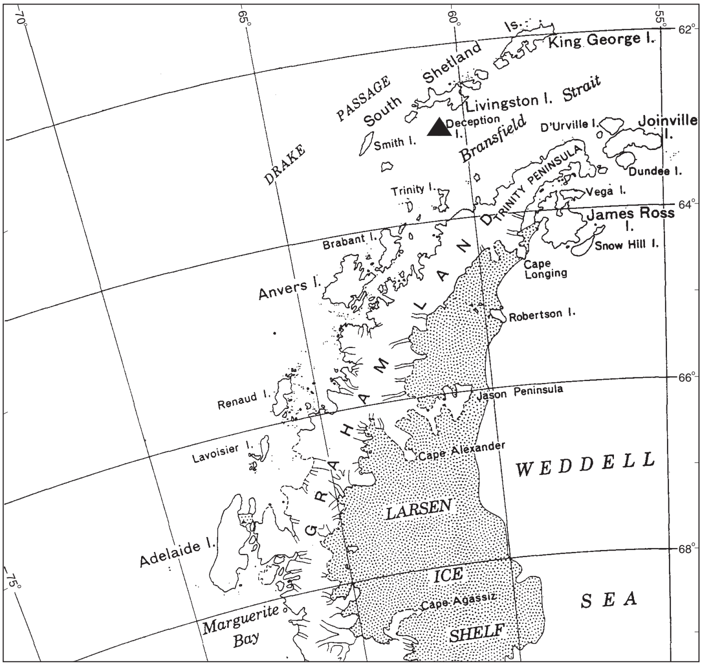

FIGURE 96. The locality of *Marchantia polymorpha* in the Antarctic based on the literature record by Young and Kläy (1971).

ispheres, but in the tropics it does not occur in the lowlands and therefore it is absent from large expanses of tropical South America, Africa, Arabian Peninsula, India and Australia (Fig. 95).

Distribution in Antarctica. — This species has been reported only once. Young and Kläy (1971) collected it as a recent colonist on Deception Island, shortly after the 1969 eruption (Fig. 96). Unfortunately, no voucher collections have been located and examined. Because *M. berteroana* was the only species subsequently recorded from this island (Lewis Smith, 1984*b*, *c*, 1988*d*) and, considering its close similarity to *M. polymorpha*, it is likely that this literature record should correctly refer to the former species. Indeed, in 1982 this author collected *Marchantia berteroana* from the same site as that where *M. polymorpha* was collected by Young and Kläy (1971). Until the specimens become available for investigation, the occurrence of this species must be considered to be doubtful. It is known, however, on South Georgia (probably as an introduced species) and in Tierra del Fuego (Hässel de Menendez, 1962, 1977).

Specimens examined. — None.

Literature records. — SOUTH SHETLAND ISLANDS: Deception Island (Young & Kläy, 1971: 359; Ochyra & Váňa, 1989*b*: 219; Lewis Smith, 1991: 322; 1993: 322; 1996*b*: 142).

GLOSSARY

abaxial — facing away from the stem or axis; opposite to *adaxial*.
acrogynous — with archegonia produced at the apex of a stem or branch, accompanied by loss of apical cells and termination of further shoot growth; opposite to *anacrogynous*.
***Acromastigium*-type branch** — a terminal branch replacing the underleaf.
acuminate — long and tapering to a narrow point at an angle of less than 45°.
acumen (pl. **acumina**) — slender tapering point.
acute — sharp-pointed with terminal angle between 45° and 90°.
adaxial — facing towards the stem or axis; opposite to *abaxial*.
air-chamber — intercellular air-containing cavities in most complex thalloid Marchantiales, usually opening to the surface by specialised pores.
alternate — of two leaves inserted at different levels on opposite sides of the stem; opposite to *opposite*.
amphigastrium (pl. **amphigastria**) — underleaf.
anacrogynous — with archegonia produced in a lateral position on a stem, branch or thallus without loss of apical cell function; opposite to *acrogynous*.
***Andrewsianthus*-type branch** — a lateral-intercalary branch arising from the antical part of the lateral segment; synonym *Anomoclada*-type branch.
androecium (pl. **androecia**) — antheridia and surrounding bracts.
angular — strongly angled, with prominent angles; synonym *angulate*.
angulate — with prominent angles; synonym *angular*.
anisophyllous — having lateral leaves much larger than or different in form from underleaves.
***Anomoclada*-type branch** — lateral-intercalary branch arising from the antical part of the lateral segment; synonym *Andrewsianthus*-type branch.
antheridium (pl. **antheridia**) — male reproductive organ composed of a spherical or ellipsoidal body with spermatozoids exserted on a short or long stalk.
antical — leaf margin oriented towards the shoot apex of a longitudinal or obliquely inserted leaf; opposite to *postical*.
antically secund — referring to leaves or bracts directed upwards or forwards to beyond the postical side of the axis.
apiculus (pl. **apiculi**) — short, abrupt point.
apiculate — abruptly short-pointed.
appressed — closely pressed against the stem.
approximate — near to each other but not touching or overlapping.
archegonium (pl. **archegonia**) — flask-shaped female reproductive organ consisting of a long neck and a venter with an egg.
arcuate — curved like a bow.

areolate — referring to a network of small, angular or polygonal areas differing in colour or structure from the surrounding area.
areolation — cellular network of a leaf.
ascending — growing upwards at an angle to horizontal.
asexual reproduction — regeneration by means of specialised structures such as gemmae or caducous leaves and branches.
attenuate — narrowly tapered.
auricle — small ear-like lobe on thalli.
auriculate — with auricles.
autoecious — with antheridia and archegonia in separate inflorescences on the same plant.
axil — angle between the leaf base and the stem.
axis (pl. **axes**) — main stem of a foliose plant.

***Bazzania*-type branch** — lateral-intercalary branch arising from the ventral segment.
biconvex — convex on both sides.
bidentate — terminating in two teeth.
bifid — forked, divided into to lobes to more than half the total length.
bilobed — divided into two lobes to about half the total length.
biseriate — arranged in two rows.
bistratose — composed of two layers of cells.
bordered — having margins differentiated from the rest of the leaf in shape, thickness, size or colour of cells.
bract — modified leaf associated with a gametangium or gemma-cup.
bracteole — modified underleaf associated with a gametangium.
branch — lateral extension of the stem.

caducous — regularly falling off; relating to deciduous branches, leaves or leaf apices which may serve as vegetative propagules.
caespitose — growing in low densely matted cushions, mats or turves.
calyptra (pl. **calyptrae**) — thin protective cover over the developing sporophyte derived from the archegonial venter and neck after fertilisation.
canaliculate — chanelled lengthwise.
capsule — uppermost part of a sporophyte containing the spores and elaters.
chlorophyllose — green, containing chloroplasts.
chloroplast — green plastids containing chlorophyll.
cilium (pl. **cilia**) — delicate, thread-like, unbranched structure mostly one cell wide.
ciliate — possessing cilia.
clavate — club-shaped, thickened towards the apex.
collenchymatous — with cell walls heavily thickened in the corners.
complicate-bilobed — bifid leaf with the lobes sharply folded together longitudinally.
compound pore — aperture surrounded by rings of strongly modified cells arranged in 5–6 superimposed circles.
concave — curved inwards like the interior of the circle.
conchiform — shell-shaped.
conduplicate — strongly folded lengthwise along the middle.
confluent — merging.
conical — cone-shaped.
connate — fused, joined together.
connivent — approaching or meeting at the tips, directed to a single point, converging.

contiguous — touching each other but not overlapping.
convex — curved outwards like the exterior of the circle.
convolute — rolled up longitudinally.
cordate — heart-shaped.
cortex — outer layer(s) of cells of the stem surrounding the medulla.
costa (pl. **costae**) — longtitudinal, multistratose median part of a thallus sharply or weakly differentiated from the laminae.
crenate —with rounded teeth.
crenulate — with minute rounded teeth.
crispate — irregularly waved, curved, contorted or undulate.
cruciate — cross-shaped.
cucullate — hooded or hood-shaped.
cuneiform — wedge-shaped.
cupulate — cup-shaped.
cuspidate — ending abruptly in a stout, rigid point.
cuticle — non-cellular covering on the external walls of cells.
cuticular — pertaining to a cuticle.
cylindrical — elongate and circular in transverse section.

decolorate — colourless; appearing hyaline.
decurrent — with the margins extending down the stem below the leaf insertion as ridges or narrow wings.
decurved — broadly curved downwards or backwards towards the postical surface or the substrate.
dehiscence — spontaneous splitting of the capsule wall to realease the spores and elaters.
deflexed — curved outwards; opposite to *inflexed*.
dentate — with sharp teeth, usually comprising one or more cells.
denticulate — minutely dentate.
dimorphic — occurring in two forms.
dioecious — with archegonia and antheridia on separate plants.
distal — away from the base or point of attachment.
distant — clearly separated from each other, spaced apart.
divergent — spreading from each other.
dorsal — upper surface of a thallus, or the surface away from the substrate.
dorsiventral — flattened, with distinct upper and lower surfaces.
dorsiventrally compressed — flattened on the antical and on the postical side.

edentate — without teeth on the margin.
elatophore — cluster of elaters attached to the base or apex of a capsule.
elater — elongate cell with one to three helicoidal wall thickenings, found intermingled among the spore mass.
ellipsoidal — three-dimentional equivalent of elliptical.
emarginate — with a broadly rounded apex, often with a small indentation.
endogenous — originating from internal rather than superficial cells or tissues.
entire — margin of leaf without teeth or lobes, more or less smooth.
ephemeral — short-lived.
epidermis — single layer of cells at the surface.
epidermal — referring to an epidermis

erect — with the leaves aligned almost parallel to the stem or the plants oriented perpendicularly to the substrate or to a horizontal stem.
erecto-patent — spreading from the stem at an angle between 20° and 45°.
erose — irregularly notched or ragged, frequently caused by abrasion of lamina.
exserted — projecting and exposed.

falcate — sickle-shaped.
fasciculate — bunched together, in bundles.
female — of an inflorescence or plant which bears archegonia.
filament — thread-like uniseriate structure.
filamentous — pertaining to a filament; synonym *filiform*.
filiform — slender and elongate structure; synonym *filamentous*.
fimbriate — fringed.
flaccid — soft, limp
flagelliform — leafy stem gradually attenuated or flagellum-like towards the apex.
flagellum (pl. **flagellae**) — slender, microphyllous branch.
flexuose — slightly and irregularly bent, twisted.
foliose — leafy or leaf-like.
***Frullania*-type branch** — terminal branch replacing the postical half of a lateral leaf and leaving the antical half-leaf.
furcate — forked.
fusiform —spindle-shaped, narrow and tapered at both ends.

gametangium (pl. **gametangia**) — vessels bearing gametes e.g. antheridium and archegonium.
gametoecium (pl. **gametoecia**) — gametangia and surrounding bracts.
gametophyte — dominat, haploid and sexual generation consisting normally of leafy or thalloid plants bearing antheridia and archegonia.
gemma (pl. **gemmae**) — uni- or multicellular specialised body mainly borne on leaves and thalli, serving in asexual reproduction.
gemmiferous — bearing gemmae.
gibbous — swollen or bulging on one side.
glabrous — smooth, not papillose, rough or hairy.
globose — spherical.
granular — roughened with minute, blunt projections.
gregarious — growing together in loose tufts or mixed mats.
gynoecial branch — specialised archegonia-producing branch.
gynoecium (pl. **gynoecia**) — female inflorescence, consisting of archegonia and the surrounding bracts.

hairs — unicellular tubular structures arising between cells of the thallus in the Metzgeriaceae.
heteroecious — with several forms of gametoecia on the same plant; synonyms *polyoecious*, *polygamous*.
hispid — bristly, with short stiff hairs.
horizontal — referring to the orientation of a structure when its plane lies nearly parallel to the surface of the axis.
hyaline — colourless, clear and translucent.
hyalodermis — differentiated external cells, e.g. enlarged, thin-walled cells of stem.
hyphae — microscopic fungal threads which are sometimes present in cells of a stem or thallus.

imbricate — closely appressed and overlapping like roof tiles.
incised — deeply and narrowly cut into sharp lobes separated by a sinus.
incrassate — with thickened cell walls.
incubous — arrangement of leaves in which the antical margin of a leaf is nearer the stem apex and often overlaps the postical margin or keel of the leaf in front; opposite to *succubous*.
incumbent — not appressed, loosely overlying.
incurved — curved upwards or inwards; referring to leaf tips or margins; opposite to *recurved*.
inflexed — turned abruptly or bent inward; opposite to *deflexed*.
inflorescence — groups of antheridia or archegonia, or both, together with the associated bracts.
innovation — new shoot produced below the perianth for continuation of growth following the development of archegonia.
insertion — line of attachment of a leaf to a stem.
intercalary — inserted between the base and the apex of a stem
intercalary branch — branch developing considerably below the apical region of a stem or thallus; opposite to *terminal branch*.
involucre — protective sheath surrounding one or more antheridia or archegonia, or a developing sporophyte, replacing the perianth or occasionally additional to it.
isodiametric — about as broad as long; applying to cells about the same diameter in all directions.
isophyllous — having lateral leaves and underleaves of the same size and shape; opposite to *anisophyllous*.

julaceous — smoothly cylindrical and worm-like in appearance; refers to stems and branches with strongly imbricate leaves.

keel — commisure or line of the sharp fold separating the antical and postical lobes of a complicate-bilobed leaf or the sides of a perianth.
keeled — sharply folded like a keel of a boat, V-shaped in transverse section.

laciniate — dissected into fine, deep, irregular lobes bearing cilia and teeth (*laciniae*).
lamina (pl. **laminae**) — part of a leaf below the lobes or the whole of an unlobed leaf; the thin or thinner expanded part on each side of a costa of a thallus.
lanceolate — lance-shaped, narrow and tapered from near the base, about three times as long as wide.
laterally compressed — flattened towards the stem on both sides.
lax — loose; referring to shoots loosely arranged or leaves spaced far apart.
leaf — chlorophyllose outgrowth from a stem, not associated with sexual organs.
lenticular — lens-shaped.
leptodermous — uniformly thin-walled.
linear — very narrow, elongate with nearly parallel sides, three or more times longer than wide.
lingulate — tongue-shaped; oblong with a somewhat broadened apex.
lobe — any segment of a divided leaf or thallus, or each of the whole antical and the whole postical part of the leaf in the Scapaniaceae.
lobulate — bearing small lobes.
longitudinal — arrangement of a leaf in which the insertion line is nearly parallel with the stem; opposite to *transverse*.
***Lophozia*-type branch** — lateral-intercalary branch arising from the postical half of a lateral segment; synonym *Plagiochila*-type branch.
lunate — crescent-shaped; curved like a crescent moon.

male — of an inflorescence or plant which bear antheridia.
medulla (pl. **medullae**) — internal cells of a stem or a seta tissue surrounded by a cortex.
medullary — referring to a medulla.
meristem — localised region of growth or potential growth by cell division.
merophyte — referring to a segment cut or divided from the apical cell and all tissue and organs derived from it by subsequent divisions.
***Microlepidozia*-type branch** — terminal branch replacing the antical half of a lateral leaf and leaving the postical half-leaf.
microphyllous — small-leaved; bearing leaves which are minute relative to the normal lateral leaves.
monandrous — with one antheridium.
monoecious — with antheridia and archegonia borne on the same plant.
mucilage — gelatinous secretion capable of absorbing and holding water.
mucilage cell — specialised cell containing mucilage on a leaf margin or scattered within a thallus; synonym *slime cell*.
multifid — divided many times.
multiseriate — arranged in several to many rows.
multistratose — consisting of several to many layers of cells.
mycorrhizal — infected with fungal hyphae (mycorrhizae).

nodular thickening — radial thickenings on a cell wall seen in surface view as knob-like protuberances.
nodular trigones — large, irregularly rounded thickenings at the corners of cells
nodulose — with minute knobs.

obcordate — heart-shaped apex with two broadly rounded lobes.
oblique — slanted; describing the insertion line of a leaf between transverse and longitudinal.
obloid — three-dimentional equivalent of oblong, with rounded edges and corners.
oblong — much longer than broad with rounded corners or ends.
obovate — egg-shaped with apex broader than base.
obscure — dark, indistinct.
obtuse — broadly pointed with an angle at apex more than 90°.
oil-body — translucent or opaque intracellular structure containing terpenes bounded by a delicate membrane; rarely persistent.
opaque — dark, not transparent or translucent.
opposite — of two leaves inserted at the same level on each side of the stem; opposite to *alternate*.
orbicular — nearly circular in outline.
ornamentation — pattern on the surface of a spore formed by papillae, spines or lamellae.
oval — broadly elliptical.
oval-oblong — with one side curved and the opposite side nearly straight; with the free margin curved and the keel straight.
ovoid — three-dimentional equivalent of ovate; egg-shaped, widest below middle and about twice as long as wide.

papilla (pl. **papillae**) — minute, solid protuberance on the surface of a cell wall or on the exine of a spore.
papillose — covered with numerous papillae.

paraphyllia — simple or branched ciliate or lamella-like appendages scattered among the stem leaves.

paraphysis (pl. **paraphyses**) — minute, mostly filiform or lanceolate structures intermixed with antheridia or sometimes in the axils of adjacent leaves.

parenchymatous — pertaining to tissue composed of undifferentiated, thin-walled cells.

paroecious — with antheridia and archegonia in a single gametoecium but not mixed, the antheridia in the axils of bracts just below the bracts surrounding the archegonia.

patent — spreading from the stem at an angle of 45° or more.

paucidentate — with a few teeth.

pellucid — clear, translucent or transparent.

peltate — shield-like.

pendulous — hanging, pendent.

perianth — tube surrounding a developing sporophyte or a low ring enclosing the archegonia, formed through the fusion of 2–3 leaves or, subsequent to fertilisation, from the thallus tissue in the Metzgeriales.

perigynium (pl. **perigynia**) — fleshy, multistratose tubular sheath surrounding the archegonia and developing sporophyte, derived from peripheral axial tissue elevating the perianth and the female bracts.

persistent — long-lasting.

pinna (pl. **pinnae**) — primary division of a thallus.

pinnate — with numerous spreading branches produced ± regularly on either side of the stem and thus resembling a feather.

pitted — with small depressions or holes in the cell walls.

***Plagiochila*-type branch** — lateral-intercalary branch arising from the postical half of a lateral segment; synonym *Lophozia*-type branch.

plano-convex — referring to the thallus or the stem which is flat above and convex below in transverse section.

plica (pl. **plicae**) — fold or pleat.

plicate — folded into several longitudinal furrows or pleats.

plurilobate — divided into many lobes or segments.

polyoecious — see *heteroecious*.

polygamous — see *heteroecious*.

polygonal — with many angles.

pore — small opening in the dorsal epidermis of a thallus surrounded by specialised cells.

porose — having pores.

postical — leaf margin oriented towards the base of a longitudinal or obliquely inserted leaf; opposite to *antical*.

postical branches — intercalary branches arising in the axil of an undeleaf.

postically secund — referring to leaves or bracts directed downwards or backwards to beyond the postical side of the axis.

procumbent — spreading, prostrate; lying flat and scarcely or loosely attached to the substratum.

propagule — vegetative reproductive structure (e.g. gemma, caducous leaf, etc.) capable of producing a new plant.

prostrate — creeping; lying flat on and closely attached to the ground.

protandrous — referring to monoecious plants on which the antheridia mature and release spermatozoids prior to the maturation of the archegonia.

protonema — a thread-like, globose or thalloid growth resulting from germination of spore or specialised asexual reproductive structure, usually giving rise to a single gametophyte.

proximal — near the base or point of attachment.
pseudoperianth — hyaline, unistratose, beaked sheath around each sporophyte and its calyptra in the Marchantiales.
pyriform — pear-shaped.

quadrate — square or nearly so.
quadrifid — divided into four ± equal lobes.

radial — aligned at right angles to the margin of a leaf.
receptacle — disc or wart-like mass of tissue bearing antheridia and archegonia situated directly on or inside the thallus or elevated and terminating a gametangiophore.
recurved — curved downwards or backwards; referring to leaf tips or margins; opposite to *incurved.*
remote — distant, widely separated.
reniform — kidney-shaped.
repand — with wavy margin.
reticulate — netted, as the network pattern produced by the cell wall thickenings.
retuse — slight indentation or notch in a broad, rounded apex.
revolute — rolled downward and backward, referring to a leaf margin.
rhizoid — delicate, unicellular tubular extension of an external cell, arising postically or ventrally, serving to anchor the gametophyte to the substrate.
rhizoid grooves — one or two longitudinal furrows containing rhizoids on the ventral side of a receptacle stalk.
rhizome — slender, horizontal, subterranean stem giving rise to erect secondary stems; synonym *stolon.*
rhomboidal — oblong-hexagonal.
rotundate — round.
rounded-quadrate — nearly square with rounded corners.
rudimentary — incompletely developed, vestigial.

saccate — abruptly and deeply concave, forming a sack.
saprophytic — living on dead organic matter.
scales — linear appendages of the stalk of male and female receptacles in the Marchantiales or ± connate structures replacing the perianth in the Gymnomitriaceae.
sclerenchyma — tissue composed of cells with strongly thickened walls.
sclerenchymatous — referring to sclerenchyma.
secondary branch — any branch arising from a main branch.
secund — directed to one side.
semiannular thickenings — U-sphaped, band-like thickenings extending over tangential and radial walls of the inner strata of capsule walls.
serrate — bearing short, sharp teeth directed towards the apex.
serrulate — minutely serrate.
sessile — without a stalk.
seta (pl. **setae**) — delicate stalk of the sporophyte connecting the foot and the capsule, usually extending rapidly by cell elongation as the spore matures.
setaceous — bristle-like.
shoot — main, leaf-bearing axis or any leafy branch.
simple — unbranched.
sinuate — plane leaf margin wavy in outline.

sinus — notch or indentation between two lobes.

slime papilla — mucilage-secreting cell.

spicate — spike-like structure.

spiciform — male inflorescence gradually tapering like a spike.

spiniform — resembling a spine.

spinulose — with numerous minute spines.

spinose — with sharp pointed teeth.

spore — reproductive structure produced in the capsule of a sporophyte which is capable of producing a gametophyte after germination.

sporophyte — diploid and asexual generation consiting of a seta, foot and capsule, remaining attached to and partially dependent on a gametophyte, initiated by the fertilization of an egg and producing haploid spores in a specialised capsule.

squarrose — spreading from the stem at an angle more than 90°.

stellate — star-shaped.

stem — main axis of a foliose gametophyte.

sterile — without reproductive structures or sporophytes.

stolon — slender, horizontal, subterranean stem giving rise to erect secondary stems; synonym *rhizome*.

striae — minute, solid linear projections.

striate — marked with fine ridges or lines.

striolate — finely ridged.

suberect — spreading from the stem at an angle of 15°–30°.

subinvolucral innovation — a branch arising below or in the axil of a female bract.

subulate — slenderly long-acuminate.

succubous — arrangement of leaves in which the postical margin of a leaf is nearer the stem apex and may lie under the antical margin or keel of the leaf in front; opposite to *incubous*.

synoecious — with antheridia and archegonia intermingled in the same inflorescence.

tangential — referring to the lengthwise dimension of cells along or round the margin of a leaf or bract.

terete — narrowly cylindrical, rounded and smooth in transverse section.

terminal branch — branch developed at the apex of a stem or thallus, the associated leaves or underleaves are often modified by branch formation; opposite to *intercalary branch*.

tetrad — group of four spores.

thallus (pl. **thalli**) — dorsiventrally flattened gametophyte not differentiated into a stem and leaves.

thallose — referring to a thallus.

tooth — small, unicellular or of several cells, ± triangular projection on a margin or apex.

tortuouse — irregularly bent or twisted.

transverse — arrangement of a leaf in which the insertion line is at right angle to the stem; opposite to *longitudinal*.

trifid — divided into three almost equal lobes.

trigones — triangular or circular wall thickenings of cells at the point of contact of three or more cells.

trigonous — three-sided in transverse section.

truncate — abruptly cut-off or squared-off at the apex.

underleaf — variously modified leaf on the postical surface of a stem or branch, usually much smaller than and differing in shape from lateral leaves.

undulate — referring to a surface or a margin which is wavy.
uniseriate — arranged in one row.
unisexual — with antheridia and archegonia borne on separate plants.
unistratose — composed of a single layers of cells.
unspecialised — pertaining to a seta or stem consisting of numerous rows of similar cells.

valve — one of the sections into which the capsule of most liverworts and hornworts and rarely mosses separates after dehiscence.
ventral — lower side of a prostrate shoot or thallus next to the substrate.
ventral scales — thin and small appendages along the ventral surface of a thallus.
ventricose — bulging on the lower side.
verrucose — covered with small wart-like projections (of cuticle), roughened.
verruculose — irregularly roughened.
vertical — orientation of an appendage when the whole of its surface faces the stem.
vitta (pl. **vittae**) — longitudinal strip of longer and often thicker-walled cells in a leaf lamina resembling a costa but only one cell layer thick.

wart — small elevation or protuberance.
wing (adj. **winged**) — lamina of the thallus or a thin longitudinal extension of the keel on a folded leaf, perianth or female bract.

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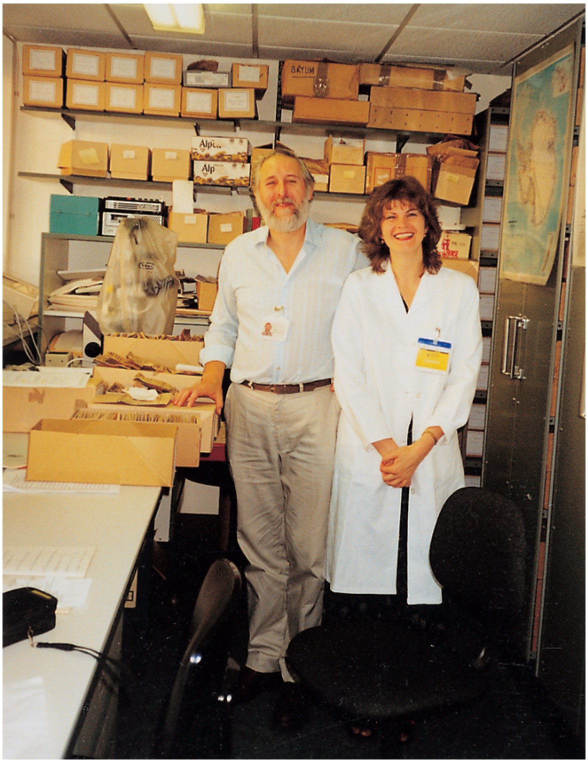

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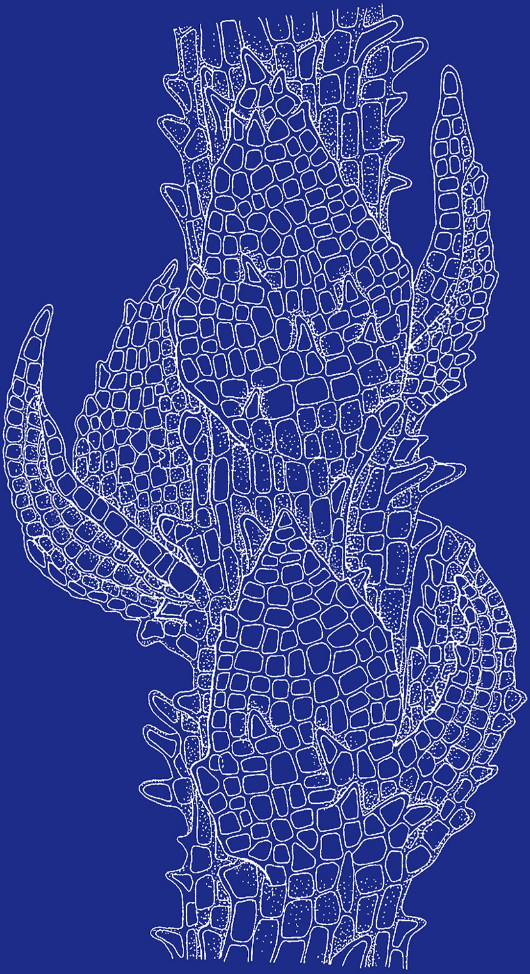

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