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A historical survey of botanical exploration in Antarctica

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Abstract

This article reviews the major botanical discoveries made in Antarctica during the last 200 years as well as the individuals who made them. An overview of Antarctic plant life is presented first. The importance of Antarctic botany is then discussed, emphasizing the field's contribution to our current understanding of biodiversity, the evolution of plant life, plant physiology and reproduction, ecology, geology, and extraterrestrial studies. Current historical problems in Antarctic botany are identified, including its slow growth and development, the scattered nature of botanical data, and the lack of a unified taxonomy. Next, the botanical discoveries and the expeditions from which they occurred are discussed. For the time period spanning 1800–1945, these discoveries are organized chronologically. Discoveries since 1945 are organized thematically, paralleling a historical shift in emphasis from exploration to science. These events are accompanied by an analysis of the political and social climate that helped shape them. Finally, some concluding remarks are made on the history and development of Antarctic botany as a scientific entity.

Introduction

The aim of this work is to review the explorations that have contributed most to our understanding of Antarctic botany, as well as the people and circumstances behind them. Impetus for this project came from the surprising lack of a solitary up-to-date work that comprehensively covered the nearly 200-year history of Antarctic botany. Due to the scope of the topic, I have chosen to broadly overview the accomplishments of the last two centuries. Readers interested in a certain expedition, geographical location, or particular time period can use this work as a convenient starting point for more detailed explorations. To this end I have placed all expedition names in **boldface** for easy location. Additionally, Table 1 lists major milestones in the history of Antarctic botany and will, I hope, serve as a handy reference and as a timeline. My wish for readers is that they not only will better understand the history of Antarctic botany but also appreciate the richness of a subject that may at first seem lackluster.

To achieve this aim, I establish a context by covering some natural history of the continent and several historical issues inherent to Antarctic botany and then examine the discoveries themselves. As these studies are too numerous and rich to be respectfully treated, some restrictions have been made to narrow the scope of this article. First, this article will only cover explorations of mainland Antarctica and islands immediately off the peninsula. These lands will hereafter be referred to collectively as "Antarctica." All other "Antarctic" lands will be excluded. Included and excluded lands are shown in Map 1, with more detailed depictions of some included regions in Maps 2 and 3. Second, I will be using a very broad definition of "botany" in this work. Cyanobacteria, algae, lichens, bryophytes, and vascular plants will all be covered; however, more stress will be placed on the latter three groups. Finally, while the emphasis of this work is on the history of botanical *explorations* of Antarctica, I will also summarize the history of Antarctic botanical *science* up to the present date.

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Table 1. Milestones in the history of Antarctic botanical exploration.

Event	Attributee	Year
First Antarctic plant sighting (*Deschampsia antarctica*)	Youngs	1819
First fossil specimen of Antarctic island flora	Eights	1830
First plant specimen of Antarctic island flora	Eights	1830
First botanist in Antarctica	Hooker	1840
First plant specimen of Antarctic continental flora	Borchgrevinck	1895
First fossil specimen of Antarctic continental flora	Ferrar	1901–1904
First non-woody fossil specimen from Antarctica	Nordenskjöld	1902
First sighting of *Colobanthus quitensis*	Turquet	1903–1905
First plant introduction "experiment" on continent	*Terra Nova* Exp.	1910–1912
First recognized *Glossopteris* fossils†	Wilson and Scott	1912
Southernmost plant sighting (a lichen)	Siple	1934

†Ferrar had actually found *Glossopteris* fossils during the British National Antarctic Expedition (1901–1904), but they were entombed in the rocks he brought back and not discovered until the late 1920s.

Plant life in Antarctica

Antarctica is first and foremost a desert—most of the water is in an unusable state for plants (ice and snow). Precipitation, primarily in the form of snow, ranges from 200–600 millimeters a year on the coast to less than 20 millimeters a year in some areas (Hansom and Gordon 1998). Ice covers most of the continent, leaving only a minute percentage of the rock surface exposed for plant life. Other factors that make Antarctica inhospitable for plants include: light periodicity, quantity, and quality; water availability; snow; temperature and other cold stresses, especially freeze/thaw cycles; and soil conditions (reviewed in Alberdi et al. 2002). Due to the large extent of ice coverage, flora is distributed mainly along the coasts and mountain slopes of the mainland and offshore islands. Coastal vegetation and mainland vegetation often differ markedly.

Most Antarctic plant communities are made up of mosses, lichens, algae, and bacteria growing together in microclimates of favorable conditions (Moss 1988; Rudolph 1971). They are often low in productivity and species richness, with members being of short stature and low biomass. Frequently, communities are composed solely of cryptogamic species (Friedmann 1982). Lichens and mosses are able to tolerate the rigors of the Antarctic climate better than angiosperms or liverworts; consequently, the former are found much further south than the latter.

Unlike all other continents, Antarctica's dominant life form is the lichen (Øvstedal and Lewis-Smith 2001). Lichens may be found on rock surfaces, within crevices, or as endolithic microorganisms. Of the approximately 200 lichen species that grow in Antarctica, *Usnea*, *Alectroia*, and *Umbilicaria* are the most abundant genera.

Antarctica also supports macrofungi, mosses, and liverworts. Twenty-eight species of macrofungi have been recognized from Antarctica (Hansom and Gordon 1998). Roughly 85 moss species can be found, with *Grimmia antarctica* being the most widely

Map 1. Antarctica, showing locations of major place names in the text. Shaded landmasses are excluded. Only mainland Antarctica and islands immediately off its coast are included in this article. Thus, the South Shetlands and the western peninsular islands are included while the South Orkney Islands and landmasses further away (such as South Georgia and the South Sandwich Islands) are excluded.

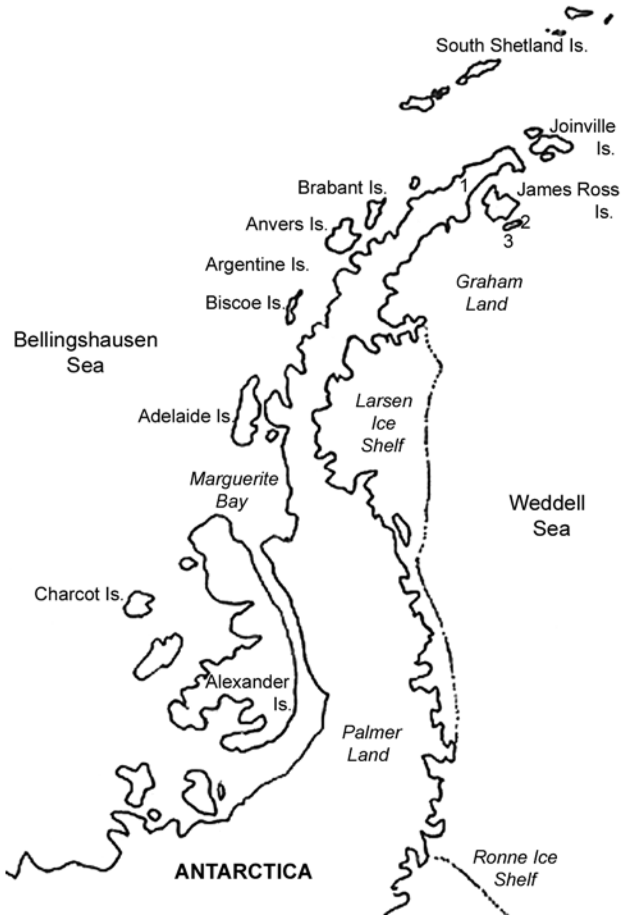
distributed. *Bryum*, *Grimmia*, *Polytrichium*, and *Sarconeurum* are also common (Seppelt 1986). Only about 10 liverwort species, most notably *Cephaloziella exiflora*, endure the tough climate.

Two flowering plants inhabit the Antarctic mainland and its immediate islands, *Colobanthus quitensis* and *Deschampsia antarctica*, with the latter being more abundant. *Colobanthus quitensis* (formerly *Colobanthus crassifolius*), a caryophyllaceous pearlwort, is limited to the peninsula and islands surrounding it (Wace 1965). In some early studies, it was incorrectly classified as a moss (Furse 1986). *Deschampsia antarctica* (incorrectly spelled *Descampsia* by some authors) is a grass. It has also been identified as *Deschampsia elegantula* or by its earlier name, *Aira antarctica*. Both flowering plants are usually found living with mosses and lichens and can reproduce either sexually or vegetatively (Convey 1996). Two foreign grasses, *Poa annua* and *Poa pratensis*, have managed to sporadically colonize islands and the peninsula, but they have not been rugged enough to survive the harsh conditions for long periods of time (reviewed in Lewis-Smith 1996).

Importance of Antarctic botany

Antarctica seems an unlikely place to be conducting botanical studies. However, despite the "poverty" of the Antarctic flora, researchers have found it scientifically fascinating for a number of reasons, each discussed briefly below. Information gleaned from the study of Antarctic botany has had a tremendous impact on multiple fields of science.

Catalogue of Antarctic biodiversity. The flora of Antarctica has an intrinsic value that early biologists attempted to capture through field notes, drawings, and herbarium specimens. Cataloguing of biota was, in fact, the chief biological activity of early explorers. While this data has been critical in our understanding of Antarctic biology and



Map 2. Detailed map of the Antarctic Peninsula. Numbered locations: 1, Louis Philippe Land; 2, Seymour Island; 3, Snow Hill Island.

global biodiversity, it has also been useful for comparative purposes. Towards the middle of the 19th century, scientists began comparing Arctic and Antarctic floras and noticing the disparity in species richness between the two groups (with the former being much richer). Questions regarding the causes of this difference are still being examined today. Botanical records and specimens also allow us to compare the Antarctica of today to what was found nearly 200 years ago. Such comparisons facilitate the identification of recently-arrived species and environmental changes.

Evolution of plant life. Antarctica's rich storehouse of plant fossils has aided our understanding of the evolution of plant life in general. Recognition of Antarctica's potential in this regard did not occur until the 20th century, mainly due to a lack of specimens. The first fossils collected were petrified wood, suggesting that life had once existed here. More detailed clues to the evolution of plant life were not discovered until expeditions started penetrating the interior of the continent (such as the coal-rich Transantarctic Mountains).

Plant physiology and reproduction. Out of necessity, Antarctic plants have acquired characteristics that allow them to tolerate the harsh conditions of the continent. Studies of these adaptations have yielded important information not only about the specific plants themselves but also about plant systems in general. These data are valuable to Antarctic scientists as well as other botanists such as horticulturalists.

Ecology. Antarctica presents a unique cold desert ecosystem that has yielded important information on the adaptability of life. Due to its low species richness in many areas, Antarctic ecosystems are much less complex than temperate or tropical ecosystems. This makes them an ideal experimental model for ecologists who can more easily parse out the contributions of various biological or environmental factors.

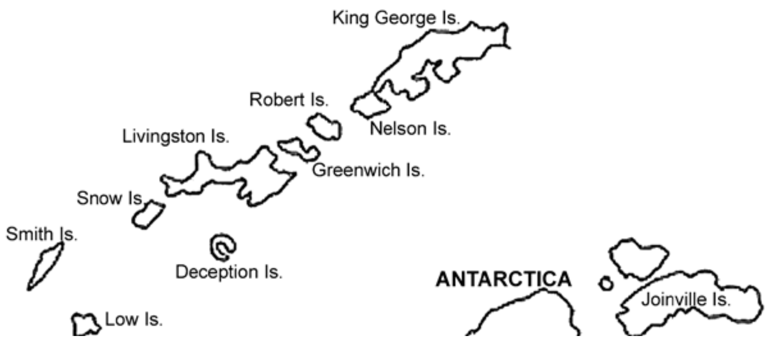
Geology. Geological studies in Antarctica have produced insights regarding the history of the continent and its past climates. These studies have also shed light on the history of the planet: Antarctic plant fossils provided the first fossil evidence of Gondwanaland and were important in Alfred Wegener's, Alexander du Toit's, and Eduard Suess' tectonic theories. For example, Wegener compared fossils of the seed fern *Glossopteris* from Antarctica to similar specimens from Africa, Australia, India, and South America to support the Gondwanaland hypothesis that all five current continents had previously been a contiguous landmass (Stanley 1992).

Extraterrestrial studies. The harsh conditions of Antarctica are similar to conditions many scientists believe may exist (or may have existed) on other planets or moons. Techniques developed to locate and analyze microbiotic life in Antarctica could thus be used in the search for extraterrestrial life (Ascaso and Wierzchos 2002).

Problems in Antarctic botany history

Several factors make it difficult for the historian to piece together the story of botanical exploration in Antarctica.

First, compared to other Antarctic sciences, botany has received considerably less time and energy. Early voyages were often commercial in nature, with scientific observations being an ancillary activity. Expeditions that did include science tended to focus more on oceanography, meteorology, or physics. Later, as science became more commonplace, disciplines such as geology and zoology tended to flourish over botany: compared to intriguing rock formations or diverse, unusual fauna, the drab, inconspicuous, and "primitive" flora of the continent was oftentimes less exciting and, seemingly, less relevant. By the time Antarctic botany had matured enough to become a field in its own right, science as a whole was caught in an updraft generated by several "new" sciences, notably, biochemistry, genetics, and experimental biology, all of which were blossoming due to new information and technologies. With the new emphases, scientists already had plenty of material, and there was no need to travel to far away, uncongenial lands such as Antarctica. Antarctic botany thus never



Map 3. Detailed map of the South Shetlands. Any islands that lie directly northeast of 57° west longitude (Elephant Is., Penguin Is., etc.) are not shown.

gained the momentum that many of the other Antarctic sciences achieved.

Second, Antarctic botanical information is fragmented. Some observations are published as scientific papers (not all of which are botanical in nature), while some are confined to expedition journals and diaries. Observations may not be published at all, surviving only as herbarium specimens and field journals. Botanical information in personal accounts is rarely organized in a format that is readily accessible to scientists, often being relegated to short sentences swamped in large paragraphs or as random comments scattered throughout massive texts. Collections are dispersed around the globe, and on more than one occasion type specimens have been lost. Furthermore, journals or specimens may still be "lost." This general inaccessibility can hamper efforts by researchers to make connections between different scientists' work and lead to considerable frustration.

Finally, the taxonomy of Antarctic plants is not unified (although efforts are underway), resulting in wildly varying accounts of species diversity and confusion in the use of scientific names. One contributing factor is the fragmented nature of the material, discussed earlier, in both geographic and temporal senses: with findings spread so widely over time as well as by collecting institution, illegitimate and misapplied names inevitably occur. Consequently, as collections are studied and organized, names often become synonyms and the number of discrete taxa decreases (Greene 1964; Hedgpeth 1971). Adding to the problem is the ambiguity of our species concept itself: not only do individuals have their own interpretations, but societal views regarding this definition have shifted during the last two centuries (Steere 1965). Also, specimens were frequently collected and/or identified by laypeople or scientists from non-botanical backgrounds. A final contributor is the paucity of type specimens for some Antarctic "species," as occasionally only a written description or drawing of the species was ever made.

Early explorations: 1819 to 1843

In 1819 Adam Young, a surgeon aboard the merchant ship ***Williams*** from England, spotted the first Antarctic plant in the South Shetlands. After landing on King George Island, the surgeon wrote:

> ... we met with no sort of vegetation except here and there small patches of stunted grass growing upon the surface of the thick coat of dung which the sea-fowls left in the crevices of the rocks, and a species of moss, which occasionally we met with adhering to the rocks themselves (Young 1821).

Several months after Young's written account, an anonymous author mentions of the same event (Anonymous 1946), "Several irregular-shaped stones and some mosses were found and taken on board."

The South Shetlands (~62° south latitude) were first spied by Dick Gerritsz around 1600 but were apparently forgotten until William Smith, one of Young's shipmates, rediscovered them in early 1819 on his way to Valparaiso (Miers 1820; Murray 1901). The *Williams* returned to the area later that same year for further exploration in the economic interests of England: waters in this region were known to contain large numbers of economically important ocean animals, such as seals and whales. Despite efforts to keep the find secret, news quickly spread. Large numbers of hunting ships soon congregated at such islands as Deception Island, which had an ideal natural harbor (vivid accounts of the magnitude of hunting are given in Charcot 1911 and Hartwig 1869).

The first biologists to reach Antarctica came on sealing and later whaling expeditions funded by private parties of their respective nations, oftentimes occupying a more critical role aboard the ship; in Young's case, which was typical of the time period, as surgeon and only tangentially as naturalist. Though the *Williams* was charged with conducting natural science during its voyage, only Young and a crewmate appear to have taken notice. Thomas Bone, the ship's draughtsman, had stayed aboard during Young's first trip out to the island but made two references to the vegetation of Penguin Island (about a mile off the coast of King George Island) that were quoted by the anonymous author mentioned previously:

> The swampy land, the lowest of all, was covered with a sort of grass and moss, nourished by the dung of the several oceanic birds; this moss and grass abounds in great quantities, and is all that deserves to be called vegetation.
>
> No land animal and no other bird were seen, except a sort of pigeon, which builds [nests] in the crevices of rocks with grass from the swamp … (Bone in Anonymous 1946).

Other botanical observations soon followed. Due to the sudden high traffic in the South Shetlands, it is not surprising that the first Antarctic plant sightings all come from this region. Richard Sherratt of the ill-fated ***Lady Trowbridge*** also noted a grass and a moss on King George Island in either late 1820 or 1821 (Lewis-Smith 1981). The **Russian Antarctic Expedition (1819–1821)** made a landing at North Foreland Cape, the spot where Smith originally landed in early 1819. Captain T. Bellingshausen (1779–1852) sent ashore three shipmates who returned with moss specimens, noting "The shore consisted of rocks covered with crumbling soil and moss; they observed no flora except the moss" (Bellingshausen 1945).

It was not until a decade after their initial sighting that the first specimens of Antarctic flora were scientifically collected. This honor goes to Dr. James Eights (1798–1882), one of several scientists funded by the Lyceum for Natural History of the City of New York who were to accompany a sealing expedition into the South Shetlands. The expedition was originally named the **Palmer-Pendleton Expedition of 1829–1831** but later was more frequently referred to as the **First U.S. Exploring Expedition**.

Eights documented from the South Shetlands two lichens and the vascular plant *Aira antarctica*, which he described as "an occasional plant of a small species of avena" (Eights 1833, p. 65). He described a moss he found as "a species of *Polytrichum* resembling the *alpinum* of Lin." (i.e., *Polytrichum alpinum* L.) (Eights 1833, p. 65). Eights is also the first to describe a fossil from Antarctica, petrified wood:

> … a fragment of carbonized wood imbedded in this conglomerate. It was in a vertical position, about two and a half feet in length and four inches in diameter: its colour is black, exhibiting a fine ligneous structure, the concentric circles are distinctly visible on its superior end, it occasionally gives sparks with steel, and effervesces slightly in nitric acid (Eights 1833, p. 64).

Besides providing the first collection of innumerable Antarctic flora and fauna for further study, Eights was also a prolific writer and gifted artist, publishing manuscripts that ran the scope of scientific disciplines. Despite all these tremendous accomplishments, Eights and his research were more-or-less forgotten until the beginning of the 20th century, by which time much of his work had been lost. His story may be found in several sources (Calman 1937; Gurney 1997; Hedgpeth 1971).

The contributions discussed thus far pertained to islands surrounding the peninsula on the western side of the continent. Initial clues about the botany of the eastern portion of Antarctica came from the French explorers

Figure 1. Jules Sébastien César Dumont d'Urville (1790–1842), photo by E. Neurdein, Paris, after a lithograph of the period, date unknown. Courtesy of Hunt Institute for Botanical Documentation.

Figure 2. Joseph Dalton Hooker (1817–1911), chalk drawing by George Richmond (1809–1896), 1855. Courtesy of Hunt Institute for Botanical Documentation.

Jules Sébastien César Dumont d'Urville (1790–1842) (Fig. 1) and Charles Hector Jacquinot (1796–1878) of the ***Astrolabe* and *Zélée* (1837–1840)**. They explored islands off the coast of Adelie Land (Queen Mary's Land) in January 1840 and declared of Point Geology "the rock was entirely bare, and did not even offer the least trace of lichens" (Dumont d'Urville 1901). The coast of Adelie Land[1] lies right on the Antarctic Circle (66° latitude) at a higher latitude than the islands discussed earlier.

Although steadily growing, Antarctic botany was practically unknown outside small circles of explorers and scientists. Like all other scientific disciplines in their infancy, it needed a champion to make it popular in the larger audiences. Joseph Dalton Hooker (1817–1911) (Fig. 2), the first botanist to visit Antarctica, fulfilled this role admirably.

Hooker's adventures in the South Polar Regions began at age 22 aboard the *Erebus*. Like Young, Hooker served as assistant surgeon first and botanist second. Robert McCormick, the chief surgeon, was in charge of all natural studies, but his disinterest in plants allowed Hooker to have full control over botanical aspects. Accompanying the *Erebus* was a second ship, the *Terror*, with its own resident botanist David Lyall (1817–1895) and surgeon John Robertson, who also served as head zoologist.

Like most expeditions before it, the ***Erebus* and *Terror* (1839–1843)**, commanded by James C. Ross (1800–1862), explored the islands around continental Antarctica. Hooker's observations from this voyage were published in his monumental work, *The Botany of the Antarctic Voyage*... (1844–1860). While containing much narrative on plants outside our geographic circumscription, the portion titled *Flora Antarctica* (1844–1847) does include some notes on the vegetation near the mainland.

Hooker first discusses the South Shetlands, acknowledging Eights' collection. Next he describes a single island situated between 64° and 65° south latitude inhabited only by lichens and algae, with no mosses or flowering plants present; in his words, "a small volcanic island, lying a few miles off the coast (Cockburn's Island)" and "close to the main portion of Palmer's Land" (Hooker 1844–1860).

Passing Victoria Land, the *Erebus* and *Terror* continued further south than any expedition before them to Franklin Island in late January 1841. Recounting their voyage, Hartwig (1869) comments: "The island … bore not the smallest trace of vegetation, not even a lichen or a piece of sea-weed growing on the rock." Thus, in a single voyage, Hooker saw a gradient from abundant vegetation (on islands near New Zealand) to reasonable vegetation (South Shetlands) to meager vegetation (Cockburn Island) to no vegetation (Franklin Island) that was a function of latitude.

While Hooker describes the genus *Colobanthus* (and *Colobanthus quitensis* in particular), his observations come from lands north of our range (Hooker 1844–1860). Thus, we cannot bestow on him the honor of being the first to recognize *Colobanthus* on Antarctica proper (this honor will not come until early in the 20th century).

Beyond standard plant collection, description, and classification, Hooker's contributions extended to the ecological realm as well. He noted that the rocks on which plants were growing provided important sources of heat for those plants, and he pointed to wind as being an important spore and seed disperser (Hooker 1844–1860). Hooker also communicated extensively with both Charles Darwin (1809–1882) and Albert Wallace (1823–1913) concerning the floral distribution of the southern hemisphere (Wace 1965). They surmised that the existence of an ancient supercontinent, which was subsequently divided into smaller lands, could account for current species distribution. In this way, Hooker laid the foundations of Antarctic plant ecology and geography. Interested readers can find a more detailed biography of Hooker in Swinton (1977).

Explorations from 1844 to 1889

Ironically, the abundance of discoveries in the early 19th century directly quelled any desire to make further discoveries in the mid-19th century. Globally, the countries that had been exploring Antarctica learned that it was a solid ice-and-land mass (and could consequently not be navigated through). Additionally, the area held limited commercial value and no prospects for settlement. More accessible lands (Africa, western America, and the Arctic) held the attention of explorers. From a scientific vantage point, physics (such as magnetism), not biology, was the thrust of earlier voyages, and the interests of those scientists had been satisfied for the time being.

As a consequence, no key botanical discoveries were made during this time. This does not imply that this period holds nothing of interest for historians of Antarctic botany. To the contrary, enough botanical exploration had been completed that scientists could for the first time begin to formulate and manipulate some of the basic themes of Antarctic botany. Writers such as Georg Hartwig (1813–1880) offer us a glimpse of prevailing notions of the time:

> Summer flowers gladden the sight of the Arctic navigator in the most northern lands yet reached; but no plant of any description — not even a moss or a lichen — has been observed beyond Cockburn Island in 64°12' S lat.; and while even

> in Spitzbergen vegetation ascends the mountain slopes to a height of 3000 feet the snow-line descends to the water's edge in every land within the Antarctic Circle (Hartwig 1869).

This quotation is notable for several features. First, it shows that scientists of the time were starting to develop a holistic concept of Antarctic botany. Second, it demonstrates that botanists were beginning to make comparisons between Arctic and Antarctic flora. These comparisons necessitated explanations. Third, the quotation shows not only what was known about Antarctic botany in 1869 but also what was *NOT* known. As will be shown, vegetation was found at latitudes further south as well as on mountain slopes of the continental interior.

Explorations from 1890 to 1899

Funding and administrative backing continued to be difficult to obtain at the end of the 19th century due to a lack of interest; however, western Europe launched three important scientific expeditions in the 1890s. I have separated the expeditions of this decade from those of the preceding periods due to their uniqueness. Compared to the preceding years, this decade represented a revitalized interest in Antarctic exploration. Though small in size, its execution paved the way for the following "Heroic Age" of Antarctic exploration. Thus, it stands alone as both different from what came before it and an initiator of what followed.

The voyage of ***Jason* (1892–1894)**, captained by the Norwegian C. A. Larsen (1860–1923), is the first of these. Larsen discovered Tertiary-age coniferous wood on Seymour Island, near the Peninsula. The fossils "…looked as if they were of deciduous trees; the bark and branches, and also the year-rings, were seen in the logs, which lay slantingly in the soil" (Larsen 1894). Even though Eights had discovered petrified wood about 50 years earlier, the intervening scientific disinterest had caused the implications of the discovery to go unattended. Larsen's find catapulted the idea that Antarctica had not always been a cold land back into scientific consciousness.

The second, and botanically most notable, expedition is that of the ***Antarctic* (1894–1895)**. After years of futile fund-raising in Australia, hampered mainly by an economic depression, the Norwegian Henrik Johan Bull traveled back to Norway to visit some contacts, and in a matter of minutes procured funding for an Antarctic expedition from Svend Foyn, world-renowned whaler. Ironically, Fogg (1992) points to whale-hunting techniques devised by Foyn as being one of the principal reasons that whalers began to hunt closer to home rather than venturing to the Antarctic during the mid-19th century. Another item of historical note is that Foyn was funding this expedition from a commercial or industrial viewpoint, whereas Bull was driven by exploratory and scientific purposes. Both individuals were mutually aware of the other's interests.

In mid-January 1894, the *Antarctic's* crew landed on Possession Island where Carsten E. Borchgrevinck (a Norwegian student) discovered lichens (Bull 1896). Several days later Borchgrevinck collected the same lichen species from the continent itself (Cape Adare, Victoria Land). These specimens constituted the first botanical specimens to be collected from the mainland itself, and for the first time allowed for comparisons of island and continental flora (for example, Fricker 1904). Bull remarked of the botanical specimens:

> The discovery of interest to most botanists was no doubt the finding on Possession Island, and later at Cape Adare, of a lichen growing sparsely in sheltered nooks. As it was previously held that no vegetation, even of the lowest order, was possible in the rigourous climate of Antarctica, this interesting lichen has created a great sensation (Bull 1896).

Beyond its contribution to botany, the *Antarctic* also showed others who were entertaining the idea of venturing back into Antarctica that the ice-belt surrounding the continent could be managed. Bull believed his voyage likely inspired several successors (Bull 1896).

The last voyage of the 19th century that bears mentioning is that of the **Belgian Antarctic Expedition of 1897–1899**. Captain F. A. Cook (1865–1940) wrote of Cape Anna, "Our greatest surprise here was the discovery of large quantities of moss and lichens, which gave the spot an appearance of life that to us, after having seen nothing but ice and black rocks for so many days, made it a true oasis" (Cook 1900). A scientist aboard the *Belgica*, Emile G. Racovitza (1868–1947), made the first record of *Deschampsia antarctica* growing on the continent itself (Danco Coast) in 1898, along with mosses and lichens on surrounding islands (Arçtowski 1901). The Polish geologist Henryk Arçtowski (1871–1958) made observations on mosses and lichens and was in many cases the instigator of collecting trips. Like Hooker before him, Arçtowski described not just the plants but also their immediate environment, demonstrating more ecological awareness than many of his predecessors, as is shown in his description of a small island off the peninsula's western coast:

> …snow uniformly covered the island. The sheet of snow gave rise to a trickle of water, forming cascades, under which an abundant vegetation of mosses and algae had accumulated. A few tufts of moss were found here and there among the stones. The sun shone strongly, and the bare rock grew quite warm (Arçtowski 1901).

Explorations from 1900 to 1914

The first two decades of the 20th century can easily be referred to as the "Heroic Age" of Antarctic exploration. This time the human invasion of Antarctica, ushered in by the voyages previously described, was motivated less by commercial incentive and more by political purpose. Explorers from different countries raced against each other to "discover" and "claim" new portions of the continent. Antarctic exploration took on an almost romantic light; heroism and patriotism were embodied in the same individuals, namely those spearheading the expeditions (readers will recognize several familiar names in the following pages). From this angle, Antarctic exploration very much mirrored what had just taken place in the Arctic. After conquering the Arctic, the world's attention naturally returned to the Southern Polar Region.

Consequential to this was a stronger emphasis on scientific exploration, as government and private bodies were now funding the voyages (as opposed to businesses or wealthy merchants of the past). From a botanical outlook, we see a shift begin to occur from simply collecting, cataloguing, and describing Antarctic plants to investigating their anatomy, ecology, and history. Reading accounts of these voyages, one is struck not only by how well organized they were, but also by the determination and resolution of the crews. Oftentimes scientific pursuits would be conducted after long sledging journeys, when everyone was exhausted and cold, their clothes wet in below-freezing weather with howling winds. That science of any nature was conducted, and to the degree that it was, is astonishing, especially considering the misfortune that frequently befell Antarctic travelers.

Headed by Captain Robert F. Scott (1868–1912) of *Discovery*, the **British National Antarctic Expedition (1901–1904)** was the longest voyage yet conducted in the Antarctic. So extensive was the planning for this voyage that a manual had been prepared for the explorers: in a short section, the manual editor discussed what flora the explorers should expect to see on the continent, and gave specific instructions on how to collect it (Murray 1901). Important collections were in fact made by the crew, specifically T. V. Hodgson and Edward A. Wilson (1872–1912), who conducted research at numerous locales around Victoria Land.

Scientific findings from the expedition were released from 1907 to 1912 in a six-volume series titled "Natural History," three of which are of particular relevance to this article: "Mosses" (Cardot 1907, vol. 3), "Lichens" (Darbishire 1910, vol. 5), and "Freshwater Algae" (Fritsch 1912, vol. 6). O. V. Darbishire noted that no new genera (only new species) had been collected from Antarctica and pointed out the existence of lichens at high elevations (1500 ft. and 5000 ft.). He highlighted the importance of lichen research in the Antarctic, lamenting the lack of scientists versed in the field as well as the need for improved preservation and shipping techniques. Felix Eugen Fritsch (1879–1954) (Fig. 3) found very few freshwater green algae on the continent; rather, a majority of the specimens (and indeed, a majority of the individual organisms) appeared to be cyanobacteria, formerly known as blue-green algae (= Cyanophyceae). Fritsch (1912) recognized the importance of his observations, naming the cyanobacteria along with *Prasiola* as being "an essential characteristic of the Antarctic flora."

Several ambiguous plant fossils were collected by H. T. Ferrar and deposited in the British Museum of Natural History. These represented the first fossils from the continent proper. The poor quality of the fossils prompted Arthur Charles Seward (1863–1941) (Fig. 4), of the *Terra Nova* Expedition (1910–1912), to describe the fossils as "not in themselves of great geological or botanical value" (Seward 1914). But what at first appeared to be a lost cause soon became an incredible find. Twenty years after their discovery, Wilfred Norman Edwards (1890–1956) (Fig. 4) suggested that some of the samples be broken open and examined, as they were not very useful in their present state (Edwards 1928). Edwards and fellow scientist F. M. Wonnacott were delighted to find not only *Glossopteris* fossils inside but also *Rhexoxylon*. The importance of *Glossopteris* is discussed later with the *Terra Nova* Expedition's discoveries, and in this light Seward's comment certainly becomes ironic. One can only speculate on the impact these fossils may have had if they had been realized earlier.

Figure 3. Felix Eugen Fritsch (1879–1954) in his office at the University of London, photo by R. D. Wood, ca.1918. Courtesy of Hunt Institute for Botanical Documentation.

Concurrent with the British National Antarctic Expedition, the **Swedish South-Polar Expedition (1901–1904)** also made important contributions to science. As was

Figure 4. Arthur Charles Seward (1863–1941) and Wilfred Norman Edwards (1890–1956) in a group photograph taken on the roof of the Botany School at the University of Cambridge, England, during a ca.1912 field trip organized by Francis Wall Oliver (1864–1951). Pictured from left to right are David Thomas Gwynne-Vaughan (1871–1915), Edward Alexander Newell Arber (1870–1918), F. W. Oliver, Mikhail Dmitrievich Zalessky (1877–1946), Agnes Robertson Arber (1879–1960), Paul Charles Edward Bertrand (1879–1944), A. C. Seward, unidentified man seated, and W. N. Edwards. Courtesy of Hunt Institute for Botanical Documentation.

customary with many expeditions, the Swedish South Polar Expedition split into several independent groups to cover more of the continent. While all three groups found plant fossils, each contributed unique botanical information.

The Captain, C. A. Larsen (of *Jason* 1892–1894), led one such group that included Carl Johan Fredrik Skottsberg (1880–1963) (Fig. 5) among its ranks. Skottsberg recorded botanical observations from the South Shetlands and the northern reaches of the peninsula. Although Skottsberg collected much paleobotanical material, his specimens were lost as *Antarctic*, crushed by floating ice, sank in waters off the coast (Nordenskjöld et al. 1977).

Otto Nordenskjöld (1869–1928), the geologist who initiated the expedition, led a second group. Nordenskjöld's party landed on Seymour Island in December 1902 and upon disembarking found the first non-woody plant fossils, embedded in the dark shale of the coast (Nordenskjöld et al. 1977). Larsen had discovered only fossilized wood on the same island in 1893. In his journal Nordenskjöld recounts that, on the following day:

Figure 5. Carl Johan Fredrik Skottsberg (1880–1963), photo by Alf. Dahlgren, Uppsala, Sweden, 1905. Courtesy of Hunt Institute for Botanical Documentation.

> I looked a long time without finding anything but fragments, until my eyes fell upon a brown, coarse, hard, tuff-like rock, and in this I at last found what I had sought for so long: numerous, large, and quite distinct leaves—although, as a rule, by no means well preserved or easily determinable—belonging to a variety of different forms of exogenous trees, firs, and ferns. It is difficult to express the joy I felt at this moment. Could it have been a dream which led me to choose just these tracts for my field of labour? For if there was one hope whose fulfillment or non-fulfillment was, in my thoughts, almost synonymous with the success or failure of the expedition, it was just that of being able to discover in these regions determinable Tertiary vegetable fossils (Nordenskjöld et al. 1977).

As can be seen from this quote and other passages in his journal, Nordenskjöld knew the importance of his find. Scientists had recognized the similarities between terrestrial organisms of Africa, Australia, and South America and sought explanations (for example, Guppy 1888). One proposal, the Gondwanaland hypothesis, was very popular but, as Nordenskjöld et al. (1977) wrote, "No proof of the correctness of such a hypothesis had been discovered before the advent of our expedition to Antarctic regions." This expedition provided the first of such proof.

The Swedish South Polar Expedition's leader, J. G. Andersson (1874–1960), led the third and final group. In January 1903, as they were trekking along Hope Bay in Louis Philippe Land, fossils of cycads, ferns, and pines were discovered. Like Nordenskjöld, Andersson also recognized how critical these specimens were: "It was evident that I had brought to light a fossil flora from the Triassic or Jurassic systems, quite a new find in South Polar regions, and one of immense importance for a determination of the former climate of the south" (Andersson in Nordenskjöld et al. 1977). Days, weeks, and months passed as the party waited for the *Antarctic*'s return, not knowing it had sunk three days before their jubilant discovery. After much waiting, they left their geological treasures behind and decided to locate help.

Andersson's crew finally met up with Nordenskjöld's team ten months later on James Ross Island, which bore poor-quality fossil-laden sandstone. Both men, encouraged by their previous finds, formulated a series of plans to recoup their losses. This started with a short sledging trip to Cockburn Island by Andersson and several companions, who found a wealth of plant fossils and, according to G. Bodman, a "verdant meadow of moss" (Nordenskjöld et al. 1977). Next, they retraced their course to Seymour Island, where bad weather resulted in an unsuccessful attempt to locate new specimens from the original search site. The shipless men continued to travel and conduct scientific investigations until they were picked up by an Argentine ship in November 1903.

Fortunately for science, the ship was able to swing by Hope Bay and collect the fossils that Andersson's party had cached earlier. These fossils, along with the results of the Cockburn Island trip, landed safely in the hands of Professor Alfred G. Nathorst (1850–1921) (Fig. 6) back in Europe (Nordenskjöld et al. 1977). Nathorst identified many genera, including *Fagus* (correctly *Nothofagus*) and specimens similar to plants found at the Straits of Magellan. Also among the specimens were exogenous trees resembling fossils from Europe and South America, ferns, and plant branches reminiscent but not the same as *Sequoia*. Summarizing the finds from his nerve-racking expedition, Nordenskjöld (1977) tells readers, "Before our expedition, no other fossils from Antarctic regions were known than the petrified tree-trunks and some shells taken home by Larsen from the north part of Seymour Island."

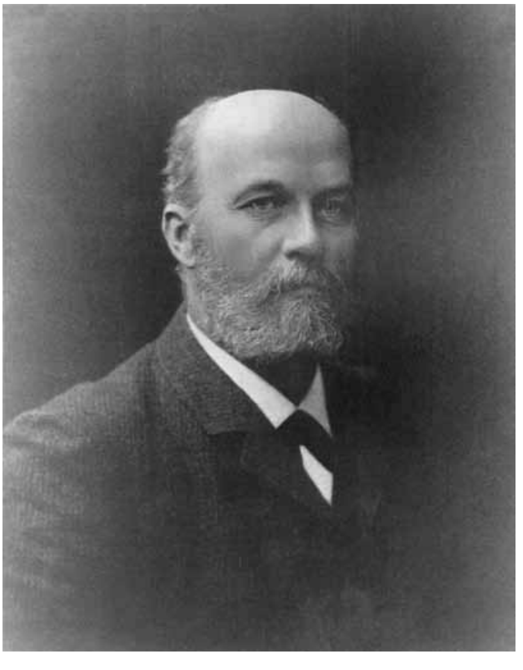


Figure 6. Alfred Gabriel Nathorst (1850–1921), photo by A. Dahllöf, 1903. Courtesy of Hunt Institute for Botanical Documentation.

One year after both the British National Antarctic Expedition and the Swedish South-Polar Expedition were underway, the **Scottish National Antarctic Expedition (1902–1904)** commenced. From this voyage, Dr. Rudmose Brown (1879–1957) made several key contributions to Antarctic botany, including observations pertaining to the identity, growth habits, and distribution of the Antarctic angiosperms, lichens, and mosses (Brown 1928).

The French also made a voyage to Antarctica in the early 1900s (**French Expedition, 1903–1905)**. Led by Dr. Jean-Baptiste A. E. Charcot (1867–1935), this voyage explored areas around the peninsula and yielded the first account of the only other native flowering plant ever discovered on Antarctica, the pearlwort *Colobanthus quitensis*, courtesy of Dr. Turquet (Lewis-Smith 1981). Turquet found that both *C. quitensis* and *Deschampsia antarctica* inhabited Anvers Island at 64° south latitude and Booth-Wandel Island at 65° south latitude (Bruce 1911).

The feverish tempo of Antarctic exploration that had started at the beginning of the 20th century continued through the first decade. More important fossil discoveries[2] were made during **Shackleton's Expedition (1907–1909).** Ernest H. Shackleton (1874–1922) had been a member on one of Scott's earlier expeditions (British National Antarctic Expedition 1901–1904) and, several years later, headed an expedition of his own. Beyond being the first to use an automobile on the continent, Shackleton's party found, in his words, the first "determinable fossil plant from Victoria Land" (Shackleton 1909).

Initially, botanical discoveries came from around camp or short excursions in the vicinity (Murray 1909). By their first summer, Shackleton's team had learned that both lichens and mosses grew at several close-by locales.

They examined the McMurdo Dry Valley Lakes and quickly appreciated their biological significance. The second summer produced more impressive results. They found rotifers and tardigrades (commonly called "water-bears") living among the mosses, and a small geological reconnaissance discovered fossilized specimens five miles from camp. Tragically, these were lost in a blizzard, but the loss was supplemented with an additional collection from the Ferrar Glacier.

Shackleton also fractured his crew into separate teams so that more of the continent could be examined. The Southern Party, of which Shackleton was a member, endeavored to reach the geographic South Pole (Shackleton 1909). On 11 December 1908, he recorded finding plant impressions and coal about 350 miles away from the Pole at The Cloudmaker (Beacon Sandstone) in Victoria Land. Despite the horrible circumstances that befell him and his crewmen, Shackleton's team lugged the heavy specimens back to base camp.

In contrast, the Northern Party was charged with reaching the magnetic South Pole (Shackleton 1909). This party made several paleobotanical discoveries and, instead of carrying the specimens along on their journey, deposited them at spots along the way with the intention of recovering them on the return trip. A journal entry for 21 October 1908 discussed one such discovery from the Beacon Sandstone:

> It contained traces of small fossils which appeared to be seeds of plants. Specimens of these were taken by us and were depôted later at another small island, which we called Depôt Island. It is much to be regretted that we were unable later to reach the depot on account of dense belts of pack-ice, and so these very interesting specimens were lost (Shackleton 1909).

The Northern Party also observed moss growing near Granite Harbour (October 28) and Cape Irizan (November 23). Lichens and moss were collected from the slopes of volcanic Mount Erebus.

Shackleton's third group, dubbed the Western Journey, was made up of Raymond E. Priestley and two companions (Shackleton 1909). On Christmas Eve 1908, they spotted a rainbow of lichens growing at different altitudes in the east fork of a glacier: a yellow lichen (3100 ft.), black lichen (3800 ft.), and a green lichen (or moss) (4200 ft.). Christmas Day brought fossilized ferns of poor quality.

Both the British and the French launched a second expedition towards the end of the first decade. In contrast to both Shackleton's Expedition and the previous French expedition of 1903–1905, the **French Expedition (1908–1910)** holds little information on Antarctic flora. Charcot's journal of the second voyage focuses mainly on the penguins, seals, and whales he and his companions observed and collected (Charcot 1911). Only two passing references are made to vegetation in his journal: 4 January (moss on Berthelot Island) and 8 February (moss on Argentine Islands).

Towards the end of the first decade of the 20th century, the Heroic Age was at its climax and had one goal in mind: attainment of the South Pole. The prospect was made even more tantalizing by the fact that several crews had tried to achieve this feat and had failed (Shackleton's expedition, for example).

One contender, likely the most widely recognized from the race to the South Pole, was Captain R. F. Scott (of the British National Antarctic Expedition 1901–1904) and his ***Terra Nova*** **Expedition (1910–1912).** In the austral summer of 1911–1912, Scott and fellow expedition members attempted to be the first to obtain the Pole on foot. When they finally reached their goal, they learned that Roald Amundsen (1872–1928) and his Norwegian crew had arrived there almost a month earlier. On top of their already poor health, the dejection that Scott and his companions felt must have been enormous. Still, Scott was convinced that their trip had not been in vain and attacked the return trip with the same vigor he had at the start. On 7 February as they descended the Beardmore Glacier, the team noticed an abundance of fossils. Scott commented that the team stopped to "geologise" on the 8th and wrote in his diary:

> We found ourselves under perpendicular cliffs of Beacon sandstone, wearing rapidly and carrying veritable coal seams. From the last, Wilson, with his sharp eyes, has picked several plant impressions, the last a piece of coal with beautifully traced leaves in layers, also some excellently preserved impressions of thick stems, showing cellular structure (Scott 1999).

More plant fossils were found on the next day, some of which the scientist E. A. Wilson (also of B.N.A.E. 1901–1904) placed in the sledge for the return voyage.

Wilson gave a detailed account of 8 and 9 February in his diary and his scientific journal. Of 8 February he described some fossils as "…long stalks of vegetable origin…from ½ to ¾ inch across, with cellular markings in cast with black crystalline coal fragments in pits" (Seward 1914). A portion of his reprinted diary for 9 February reads:

> There were to be found in many of the sandstone blocks twisted bands of coal—much contorted—and full of vegetable remains…These would be profitable for exam. But the best leaf impressions and the most obvious were in the rotten lumps of weathered coal which split up early to sheath and knife. Every layer of these gave abundant vegetable remains…(Wilson 1972).

From this point forward Scott's team was plagued with ill fortune. After losing two men during the trek back, Scott and his two remaining companions were soon forced to set up camp 11 miles away from a supply depot due to a blizzard. The unusually fierce weather continued (Solomon and Stearns 1999), prohibiting the weakened men from going any further. The three explorers passed away on 29 March after writing farewell letters in their tent.

Eight months later their bodies were discovered in a nearly snowed-in tent (Atkinson 1999). Their sledges were also found and, remarkably, contained almost 35 pounds of geologic specimens from the moraines of the Beardmore Glacier! C. L. Atkinson writes, "…at Dr. Wilson's request they stuck to these up to the very end, even when disaster stared them in the face and they knew that the specimens were so much weight added to what they had to pull." Before burying the bodies, the three men also recovered the personal diaries and scientific notes of the victims.

Scott's team obviously understood the tremendous importance of the plant fossils. Researchers later established that, among the samples, were some *Glossopteris* (Schopf 1970). Together with previous finds from South America, Africa, India, and Australia, these fossils provided the first published paleontological evidence for the Gondwanaland hypothesis. Thus, their importance reached far beyond botany into numerous other realms of science and was readily recognized by scientists of the time, even just shortly after their discovery (i.e., Seward 1914).

Members of this expedition were also the first to attempt to grow a foreign plant on Antarctic soil (Lewis-Smith 1996). Sea kale seeds, *Crambe maritima*, were sown over a moss bed; while 12 seedlings emerged, none survived more than a week. I wish to caution the reader regarding the scientific veracity of many of the early plant introductions. These "experiments" were undertaken as more of a curiosity than anything else; the casual attitudes and haphazard record-keeping of those involved render most of these observations scientifically invalid despite their intriguing nature.

From a historical perspective, it's interesting to note the discrepancies between R. Amundsen's (**Norwegian Antarctic Expedition, 1910–1912**) and Scott's teams. While Scott was determined to man-haul (i.e., have members of the team pull the sleds) to the Pole, Amundsen used dogs. Clearly, Scott's method was the harder of the two and obviously contributed to the tragedy. Another discrepancy is the importance of science on the two teams. Both groups were focused on getting to the Pole. A quick perusal of Amundsen's expedition diary shows that little science was conducted beyond meteorological observations (Amundsen 1913). In contrast, much diverse scientific work was carried out on Scott's expedition. So committed to these enterprises was Scott that he even engineered special quarters at base camp purely for science. Indeed, Scott and his companions, facing poor health and vicious weather, still devoted themselves to hauling the 35 pounds of plant fossils, which many would have readily left behind. Had Scott, Bowers, and Wilson jettisoned these fossils, they might have survived. I should also mention that while Scott and his men were trekking back from the pole, another component of his expedition (Frank Debenham [1883–1965?], Priestley [of Shackleton's Expedition 1907–1909], and others) was also discovering plant fossils elsewhere (Seward 1914).

Just as the *Terra Nova* and Norwegian Antarctic expeditions were concluding, Sir Douglas Mawson (1882–1958) and his **Australian Antarctic Expedition (1911–1914)** steamed into Commonwealth Bay, Adelie Land. After first visiting Antarctica as a member of Shackleton's Expedition, Mawson returned heading his own expedition. A main base (Cape Denison) and a smaller western base were established, and each of these in turn broke into smaller groups for exploration.

Six groups of three set out from the main base in November 1912. Mawson, Lieutenant Belgrave Ninnis, and Dr. Xavier Mertz headed out to map the far-eastern coastline; only Mawson returned, as Ninnis died in a crevasse fall and Mertz of poor health. Fortunately, the other teams experienced less harrowing treks. Frank Bickerton (1889–1954), A. J. Hodgeman, and L. A. Whetter found the first meteorite from Antarctica while exploring coasts west of the main camp. C. T. Madigan, A. L. McLean (a biologist), and P. E. Correll explored territory beyond the Mertz Glacier. On Aurora Peak (22 November), the three men found that "moss and lichens were plentiful, and McLean collected specimens"[3] (Madigan in Mawson 1914). After reaching their farthest point from base camp, the party began their return journey and soon after (likely 20 December) discovered "black, fossilized plant-remains" on the talus slopes of Horn Bluff along with a tiny sea urchin shell. McLean again collected and labeled specimens of algae, lichens, and moss, as well as the soil from which they grew. At Penguin Point (29 December), "abundant lichens and mosses" as well as "tiny insect-like mites living amongst the moss" were discovered on the summit.

Crew members from the western base also made botanical contributions. Frank Wild (1888–1969) and his companions noted lichens and moss growing on Hippo Nunatak in the Bay of Winds (Wild in Mawson 1914). The same were growing "luxuriantly" at Watson Bluff on David Island. More detail is given of Haswell Island: "Vegetable life existed in the form of algae, in the pools, lichens on the rocks, and mosses which grew luxuriantly, chiefly in the Adelie penguin rookeries." Moss collections made by C. T. Harrison (a biologist) and S. E. Jones (medical officer) were published in the expedition's Scientific Reports; five species were reported (Dixon and Watts[4] 1918).

Mawson's expedition departed from the island in December 1913 but made a quick visit to the Mackellar Islets, a clustering of small islands about two miles off Commonwealth Bay. Mawson (1914) said "Algae, mosses, and lichens made quite a display in moist localities." Fossil finds were described as "several pieces of fossilized wood and coaly matter" by Mawson (1914) and later as "carbonaceous markings" by Seward (1914).

Explorations from 1915 to 1945

The face of Antarctic exploration, and consequently Antarctic science, continued to change in the 1920s. Land claims took on heightened importance as nations found themselves in two world wars. For the first time, large numbers of military personnel inhabited Antarctica due to its strategic location. The impact of the military's presence at this time cannot be overlooked: it put Antarctica under a regulatory framework unseen before. It focused a new type and an added degree of attention and awareness on the continent. Additionally, military occupation brought with it more scientists than Antarctica had ever witnessed. Science's primary concerns at this time were still geography, geology, meteorology, physics, and zoology.

Over the first 100 years of Antarctic exploration, expeditions grew in complexity due to increased organization and planning, which was possible because of knowledge gleaned from previous expeditions. Adventurers now knew what the South Polar Region was like. Armed with this information, scientists were for the first time able to plan in advance,[5] and from this point forward we begin to see a shift in emphasis from *exploration* to *science*.

Similar to the Heroic Age, this time period also had its famous personalities. After completing the first flight to the North Pole in 1926, Richard E. Byrd (1888–1957) next set his eyes on doing the same in the Antarctic via the **(First) Byrd Antarctic Expedition (1928–1930)** (Byrd 1930). Byrd took several scientists with him to Antarctica and often provided special quarters for them at their base on the Ross Ice Shelf named *Little America*. Byrd's first expedition was a triumph in both flight and radio technology. Unfortunately, strong winds destroyed the airplane that was to be used for scientific exploration and a sledging venture was planned in lieu. In December 1929, his team discovered lichens further south than any expedition before on Mt. Nansen (between 85° and 86° south latitude) as well as coal deposits. Eleven days later they broke their own record by finding lichens even further south.

In contrast to his first Antarctic expedition, Byrd's second venture into Antarctica (**Second Byrd Antarctic Expedition, 1933–1935**) was more scientifically oriented. The expedition's extensive botanical findings were published in three separate but contiguous reports in the *Annals of the Missouri Botanical Garden*, with papers on ecology and plant distribution (Siple 1938), lichens and their parasites (Dodge and Baker 1938; the specimens examined by these two authors were collected by Siple), mosses (Bartram 1938), and even an index (Anonymous 1938). Botanically speaking, the climax of the excursion occurred 7–13 December 1934 as Paul Allen Siple[6] (1908–1968) and his party collected fossils and living plants from Mt. Weaver, an 8200 ft. mountain. Mt. Weaver is located at 87° south latitude, 152° west longitude, approximately 207 miles from the South Pole at the interior tip of the Ross Ice Shelf (Byrd 1935). Siple and his colleagues found numerous leaves, stems, trunks, and imprints of these embedded in the pinkish-white sandstone at the summit and shortly below.

Living plants were also abundant on and around Mt. Weaver. Lichens sometimes covered the exposed rock surfaces to the extent that they were "bright as paint" (Byrd 1935). Byrd wrote, "... the discovery of life existing in comparative luxuriance at such a high latitude was quite unexpected." Siple too remarked on how exciting it was to find plant life at a location so far south at such high elevation.[7] He and his associates collected specimens of these lichens, as well as mosses, algae, and microorganisms. So fruitful were the fossils and biological specimens that Byrd (1935) later commented, "... [the party was] so loaded with specimens they could hardly walk."

The party's contribution to Antarctic botany was more fully realized in the following years as their specimens were studied and compared to earlier finds. They provided us with the first insights as to the flora of the Antarctic interior. From Siple's collections and observations, it was learned that algae and associated microorganisms, fungi, lichens, and mosses made up the bulk of Antarctic flora. Earlier hypotheses that *Colobanthus quitensis* and *Deschampsia antarctica*, described as "both dwarfed and primitive and rare," would be confined to coastal regions and islands were confirmed. Science's understanding of environmental factors and how they affected plant life under extreme conditions was also greatly enriched.

Concurrent with the American Second Byrd Antarctic Expedition, the British conducted their own scientific exploration of the western coast of the peninsula (**British Graham Land Expedition, 1934–1937**). Preliminary scientific findings were published in *The Geographic Journal* (Fleming et al. 1938). In the section titled "Plants and Seals," G. C. L. Bertram gave an account of the bryophytic flora on the Argentine Islands, a land he described as "botanically the richest" of Antarctica proper. He first described a moss colony on the northern slope of a heavily-glacierized island, presumably Berthelot Island[8] because a photograph of this locale was included in the article. Bertram reported that moss colonies on this island could stretch to an acre in size, sometimes forming three-foot-deep bogs (perennially frozen save for a couple of inches on the top which thaw during the summer). Ecological observations were also recorded. Next, Bertram discussed similar, though smaller colonies, on Léonie Island further south (Marguerite Bay). *Colobanthus quitensis* was also found at this locale, but Bertram pointed out that *Deschampsia antarctica* occurred more frequently than *C. quitensis*, usually between Marguerite Bay and Deception Island. Diary accounts from the expedition (Lewis-Smith 1996) also mentioned an unidentified yet presumed alien grass on Deception Island in January 1936. Another rudimentary plant introduction experiment was attempted, this time by sowing oat and grass seeds from the homeland over moss beds on Galindez Island (near the Argentine Islands), but the experiment was never followed up.

Byrd was not the only Arctic aviator to lead expeditions into Antarctica during this period: another was Lincoln Ellsworth (1880–1951), who had flown over the North Pole with Amundsen. It is tempting to speculate that R. Amundsen's stories of the frozen south may have ignited Ellsworth's interest in the Antarctic. His first expedition occurred in 1935 and his second in 1938, but for the purposes of this article only the latter is of note. During the **Second Ellsworth Expedition (1938–1939)**, fossils were collected from Snow Hill Island (near the eastern tip of the peninsula); furthermore, Ellsworth also surmised that the island may harbor stores of petroleum (Shapley 1985).

World War II (1939–1945) erupted at the conclusion of the Second Ellsworth Expedition. Its impact on Antarctic research was profound. Prior to the bombing of Pearl

Harbor, the U.S. had sent another expedition to Antarctica, the **U.S. Antarctic Service Expedition (1939–1941).** The planned program was long-term and broad in vision, but two factors conspired to attenuate it. First was its whirlwind execution. Second, and more important, were the divergent interests of those who planned it. Byrd, who was in charge of the expedition itself, intended to establish a permanent research station on the continent, but the U.S. Congress (its major sponsor) had other ideas. Undoubtedly, the events leading up to and including the war were key influences leading to the expedition's premature termination: the U.S. maintained a strong military stance in Antarctica throughout and following the war (Shapley 1985). However, the expedition still deserves merit for its meticulous recordkeeping as well as its extensive geographic coverage. Many moss specimens were collected (Bartram 1957).

The British military launched its own program in Antarctica via ***Operation Tabarin* (1944–1946)** at the onset of World War II. Bases were constructed along the west coast of the peninsula and on surrounding islands. The botanist Ivan Mackenzie Lamb (1911–1990) (Fig. 7), a renowned lichen and moss expert, made important botanical collections from the peninsula beginning in 1943 as part of *Operation Tabarin* but continuing through the following decades (see Llano [1991] for a comprehensive biography and bibliography). Lamb had a talent for collecting and cataloguing and traveled extensively, especially in southern regions of the globe. He also had a decided streak of selfishness. To adduce, in his two-part series on "New, rare, or interesting lichens from the southern hemisphere" (Lamb 1948, 1953), Lamb spent a substantial amount of time criticizing the work of Auguste Maria Hue (1840–1917; French Expedition, 1903–1905) and Edvard August Vainio (1853–1929; Belgian Antarctic Expedition, 1897–1899).

Lamb's legacy of Antarctic lichen research is complimented by other contributions to Antarctic botany, including work with angiosperms. In February 1944, Lamb mentioned a foreign grass species growing on Deception Island that R. I. Lewis-Smith (1996) believes may be the same one that the

Figure 7. Ivan Mackenzie Lamb (1911–1990) at Port Lockroy, Antarctica, during *Operation Tabarin* (1944–1946), 30 December 1944. Courtesy of Hunt Institute for Botanical Documentation.

British Graham Land Expedition spied almost a decade earlier. Lamb also conducted plant introduction experiments that were never published: the results, culled from unpublished materials, were detailed by Holdgate (1964).

Another development of note during this time period is the establishment of Antarctic institutions. It became increasingly evident to everyone that, while there were abundant scientific records pertaining to Antarctica, these were scattered geographically, throughout all different forms of media. Thus there was a pressing need to organize this information into a cohesive whole that was readily accessible and understandable.

The short-lived International Polar Institute in Belgium (founded in the 1900s) established a model for this type of organization (Fogg 1992). Two Cambridge geologists introduced previously, Priestley and Debenham, established the Scott Polar Research Institute (S.P.R.I.) in 1920; it focused on both the collection and the cataloguing of specimens from the Antarctic. More polar institutes soon sprouted, including France's Expeditions Polaires Français (1947) and Norway's Polarinstitutt (1948).

While these institutions served admirably as physical repositories of both artifacts and information, equally or perhaps more influential were the publications they produced. Germany led the way in this respect by launching *Archiv für Polarforschung* in 1926, which was followed five years later by the S.P.R.I.'s *Polar Record*. Journals served as a mobile, comparatively cheap, and relatively permanent vehicle for disseminating information.

In 1928, the American Geographical Society commissioned *Problems of Polar Research*, a compendium of papers sampling all fields of Antarctic science. This publication was a result of the Americans' rekindled interest in Antarctica and gives historians an indication of the status of Antarctic science (including botany) in the late 1920s. In it Priestley and C. E. Tilley (1928) discussed "Geological problems of Antarctica," in which they enumerated on various paleobotanical finds to date, including fossils from Cambrian, Permo-Carboniferous/Rhetic, and Tertiary specimens. These fossils had been imperative in substantiating the Gondwanaland hypothesis (especially *Glossopteris*). The same thread is followed through Priestley and C. S. Wright's "Some ice problems of Antarctica" (1928) where they elaborate on past changes in climate and simultaneous shifts in vegetative profiles.

R. Brown (of the Scottish National Antarctic Expedition 1902–1904) proffers a direct account of Antarctic botany in "Antarctic and sub-Antarctic plant life and some of its problems" (1928), another paper in the book. Botanical specimens were at this point numerous enough that he and other botanists were beginning to make intracontinental floristic comparisons. Brown divided the Antarctic flora into three groups (endemic, Arctic, and Fuegian), each of which had its own history of arrival to the continent and elaborated:

> Probably the present flora first reached Graham Land and adjacent islands, where it showed its richest form, and then spread eastward around the rim of the continent. The migration must have been slow, for it could occur effectively only during a few weeks at midsummer when mosses and lichens "fruit" and there is bare ground for the wind-blown spores to lodge on. No doubt sub-Antarctic islands like the South Sandwich Islands, Kerguelen, and the Heard Islands helped in the process by acting as sources of supply for the continually migrating flora, which lodged on these islands in its passage (Brown 1928).

It is critical to point out here that Brown is not implying that the present-day flora is a direct descendant of ancestral flora. Rather, he opines elsewhere that the present flora must be composed of relatively recent newcomers, as past glaciations would have obliterated any former flora (thus the term "invasive species" is misleading). Other topics detailed by Brown included an analysis of Antarctic environmental factors that have impacted the present flora; why Antarctic botany had been neglected compared to other sciences; contemporary obstacles in research; and the sub-Antarctic flora. Much of what Brown wrote holds true today, although other concepts have been overturned; for example, Brown's statement that the two Antarctic angiosperms could only reproduce vegetatively has been disproven (Convey 1996; Rudolph 1971). R. C. Murphy (1928) discussed both plant and animal life in the fourth paper, "Antarctic zoögeography." Some notable differences exist between his account of the Antarctic flora and Brown's.

Antarctic botany from 1946 to present: The role of the political and social climate

My organizational scheme for the preceding sections was to discuss contributions to Antarctic botany chronologically by expedition date. However, to discuss Antarctic botany from 1946 to the present in this format would be cumbersome at best because of the changes that have taken place in the field over the course of the 20th century.

First, and perhaps most prominent, is a decrease in the number of "expeditions" to Antarctica. Voyages to this point had been aimed principally at large-scale mapping of unexplored coastlines by ship and, later, ground or aerial penetration to higher and higher latitudes. Following the achievement of the Pole by Amudsen, Scott, and their companions, subsequent explorations continued to map unexplored portions of the continent; however, due to Antarctica's relatively homogeneous nature (from the standpoint of explorers and those funding them), this quickly lost its novelty. Thus, beginning around the 1920s, the desire to explore was modified, with the goal being to explore smaller portions of the continent or surrounding islands at a much greater resolution and for more practical purposes (such as military occupation).

Second, the political climate of Antarctica changed, especially following World War II. Claims to portions of the continent (some of which were conflicting) took on new importance in light of the ensuing Cold War. Antarctica was no longer a free-for-all territory but instead a regulated continent, and the heightened involvement of governments became permanent. Overall, science mostly benefited from this transition.

Third, the nature of Antarctic botany continued to change from an emphasis on "exploration" to one more of "science," for many of the same reasons that the nature of geographical exploration changed. However, unlike geographical exploration, botanical research at this smaller scale revealed that Antarctica was anything but homogeneous.

Fourth, societal perceptions of science changed dramatically during the 20th century. Science rose to a new level of prominence that was unseen in preceding centuries. Governments funded and sent more scientists to the continent, and science itself became a catalyst for collaborations between researchers from different countries. Technological advances aided in multiple ways. Transportation breakthroughs allowed for speedier conveyance of scientists or specimens while new forms of communication facilitated faster exchange of information. Off the continent, scientific institutions became more common and more diverse with time and represented valuable sources of funding and resources.

History from this point forward has its origins in the Cold War. In the tense political atmosphere, everyone recognized that something had to be done to regulate the continent, but since nothing of this nature had ever been done before people were unsure of how to go about it. The late 1940s and early 1950s saw individual countries trying to grapple with the issue of Antarctic regulation. Most of these countries had already established a military presence on the continent. For example, Great Britain's *Operation Tabarin* became the Falkland Islands Dependency Survey (F.I.D.S.) and then the British Antarctic Survey (B.A.S.). Each country tried to regulate its own perceived area of the continent.

These "solutions" were only temporary, and the need to internationalize Antarctica loomed large. The biggest difficulty was determining who to include in this regulation and who to exclude: both casual and formal proposals were volunteered, but excluded countries frequently felt they had been unjustly ostracized (Chaturvedi 1996).

Despite the political turmoil that surrounded Antarctica, most governmental entities acknowledged that Antarctica was more valuable as a whole rather than in exclusionary pieces, and recognized that science was the ideal facilitator for such an international venture. The success of the **International Geophysical Year of 1957–1958** convinced major powers that such collaboration was at least feasible, and talks began (the Scientific Committee on Antarctic Research [S.C.A.R.] was also established at this time [Fifield 1987]).

The result was the **Antarctic Treaty of 1961** (Ensminger et al. 1999; National Research Council 1993), which had three main consequences: 1) it protected the Antarctic environment; 2) it nullified territorial claims by the signatory countries; 3) it fostered Antarctic science through diplomacy. Under this document, the twelve signatories agreed to a decentralized form of management, which shortly thereafter was subjected to and survived a political acid test resulting in the **Agreed Measures for the Conservation of Antarctic Fauna and Flora of 1964** (Chaturvedi 1996). One of the more visible outcomes of this legislation was the establishment of specially protected areas and species (S.P.A. and S.P.S., respectively). Oddly enough, there was no real scientific impetus for the Agreed Measures; rather, it was more of an exercise to gauge the true authority of the treaty.

Environmental outcomes were further strengthened in 1991 by the international **Protocol on Environmental Protection to the Antarctic Treaty** (often shortened to "Madrid Protocol" or just "Protocol"), which the United States ratified through the Antarctic Science, Tourism, and Conservation Act six years later (Ensminger et al. 1999). Importantly, both the Protocol and the National Environmental Policy Act (N.E.P.A.) govern U.S. activities in the Antarctic today.

Nourished by the sociopolitical events of the second half of the 20th century, Antarctica witnessed a burgeoning of scientific research stations. Many were converted military bases. These stations have truly been a global enterprise. For example, while New Zealand and the U.S. established Hallett Station near the Ross Sea, the Japanese constructed Syowa Base on East Ongul Island — the opposite side of Antarctica. A comparison of these ventures will give a representative view of such projects.

Syowa Base was established during the first year of the **Japanese Antarctic Research Expedition** (1957–1960). Botanical investigations were mainly exploratory in nature, as this side of the continent had been virtually neglected by scientists from the Western hemisphere. The expedition's botanical discoveries (Horikawa and Ando 1961) allowed scientists to finally consider the botany of Antarctica as a whole. Studies continued at the base following completion of the expedition, including extensive ecological studies of mosses (Matsuda 1964a, b) and plant introduction experiments (Hoshiai 1970). These investigations were the first of their kind in this region.

In contrast, Hallett Station was situated in a region that had been frequently explored and governed by countries that had occupied Antarctica for over a century. As the flora was already known, scientists turned their attention to more experimental studies. E. D. Rudolph (1966b) conducted a three-year microclimate study on algae, mosses, and lichens near the station. Combining his results with Tatsuro Matsuda's, as well as with ten years of climate data for the area (Rudolph 1966a), he concluded that macroclimactic data did not fairly represent the microclimate that Antarctic plants experienced. He also found that, of all the environmental factors, temperature was the main limiting factor.

Long-term projects such as these are ongoing, and by 1983 the Antarctic boasted 34 year-round research stations (Shapley 1985). The McMurdo Dry Valley Lakes Long-Term Ecological Research Project (L.T.E.R.) is perhaps the most notable contemporary example.

Antarctic botany from 1946 to present: Major scientific foci

In the remainder of this work, I will discuss the last 50 years of contributions to Antarctic botany. As stated previously, I have organized these contributions into several major areas of emphases including: exploration and discovery; phytogeography and ecology; physiology and reproduction; genetic studies; and paleobotanical studies. Any division of Antarctic botanical research into foci is by its intrinsic nature fundamentally artificial, as all disciplines of science are interrelated. I have chosen these foci solely for their educational value as they best convey both overall trends in Antarctic botanical research as well as individual efforts. I apologize to any botanists whose work I neglected to document due to logistical constraints. In some instances I have chosen to emphasize more recent works of a focus because they emphasize our current understanding of the topic and their bibliographies serve as references for readers interested in the histories of those specific foci.

Several recurring themes emerge from a comparison of the different foci, two of which are intricately interwoven: the accumulation of knowledge and technological advancement. Both of these changed the ways questions were formulated and answered by allowing scientists to conduct an increasing diversity of scientific studies at multiple biological levels, some of which were inaccessible at the beginning of the century. These two themes also facilitated the revision or replacement of previously held ideas. A third theme is the increased awareness of the interrelationship of scientific disciplines, which facilitated not only communication between scientists of different specialties but also led to insights that had gone unnoticed. The increasing intensity (volume) of scientific research constitutes a fourth theme. A fifth and final theme, which may surprise some, is the observation that many of the questions that held the interests of scientists at the beginning of the century are still being explored today. The study of organismal adaptations to the Antarctic climate is a prime example. These five themes are echoed throughout each of the major research foci of Antarctic botany.

Exploration and discovery. Despite the incredible accomplishments of Antarctic explorers, much of the continent has yet to be visited. Progress in Antarctic exploration has often been communicated in terms of latitude. Though dramatic and convenient, it gives a false impression about the thoroughness with which we have explored the continent because it does not consider longitude. Table 2 gives the degree of latitude of the southernmost recognized plant throughout the history of Antarctic botany. While historically informative, it illustrates the false impression I just described, as most of these discoveries were made in the same quarter of the continent.

Botanical exploration and discovery have been ongoing through the 20th century. Two discoveries in particular bear mentioning here. One major discovery has been the recognition of Antarctica's cryptogamic flora. Endolithic cyanobacteria were first visually identified in rock samples from South Victoria Land in the mid-1970s (Friedmann and Ocampo 1976). Soon it was found that a wide variety of organisms, including endolithic algae, fungi, and lichens, inhabited Antarctica's rocks and that these cryptogamic organisms could be found in geographically diverse areas (Friedmann 1982). Just recently, cyanobacteria, bacteria, and fungi were described from a previously unrecognized habitat, gypsum crusts (Hughes and Lawley 2003). A second major breakthrough was George Albert Llano's (1911–2003) (Fig. 8) midcentury discovery of hepatics from East Antarctica, a region where they had been unknown till that time (Steere 1965).

New species are continually being discovered in Antarctica, both from living and preserved specimens. To illustrate, recent investigations

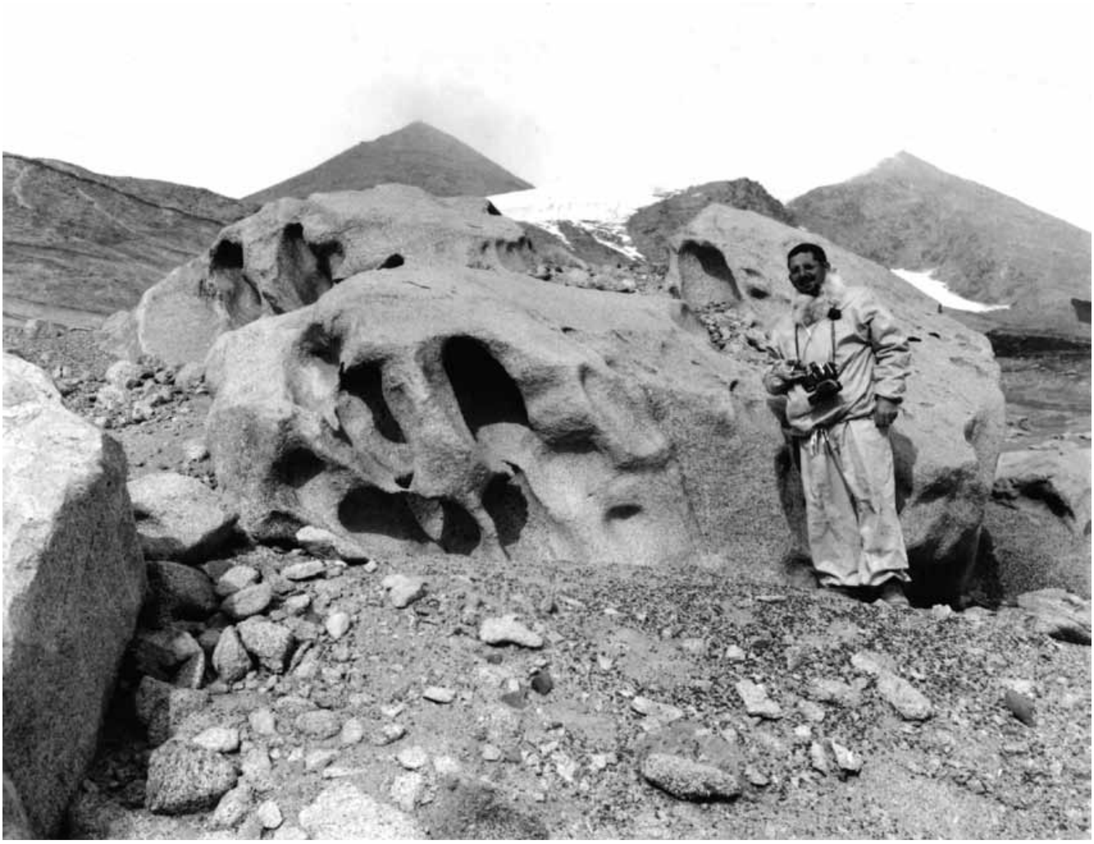


Figure 8. George Albert Llano (1911–2003) at Taylor Dry Valley, McMurdo Sound, Victoria Land, Antarctica, November 1957. Courtesy of Hunt Institute for Botanical Documentation.

Table 2. Changes in acknowledged southernmost extent of Antarctic vegetation over time, shown through a selected sample of references. Findings are organized according to organism type (note the conflicting data in "lichens"). Observations debated by historians are excluded. The degrees of latitude for places mentioned only by name (i.e., "South Shetlands") are approximated.

Organism	Author (Year)	Latitude
Angiosperms	Young (1819)	62
	Hooker (1844–1860)	61–63
	Hartwig (1869)	64
	Charcot (1909)	64
	Bagshawe (1939)	64–65
	Skottsberg (1954)	68
	Alberdi et al. (2002)	68
Lichens	Hooker (1844–1860)	71
	Hartwig (1869)	64
	Cook (1900)	66
	Gould in Byrd (1930)	85–86
	Siple (1938)	87
	Wise and Gressitt (1965)	86
	Alberdi et al. (2002)	86
Liverworts	Hartwig (1869)	64
	Rudolph (1971)	68
Mosses	Young (1819)	62
	Hartwig (1869)	64
	Cook (1900)	66
	Charcot (1909)	65
	Bagshawe (1939)	64
	Wise and Gressitt (1965)	84
	Longton (1985)	84

of the cyanobacterial mats in the McMurdo Valley Dry Lakes have turned up several new species (Reddy et al. 2002a, b). Studies such as these use a spectrum of tools to identify new taxa, from traditional morphology to biochemistry to genetic techniques.

And though they have changed substantially, expeditions are still an integral component of Antarctic botanical discovery. Sir Vivian E. Fuchs (1908–1999; an early figure in the B.A.S.), for example, discovered 105 million-year-old fern and *Gingko* fossils while tracking along the Antarctic coastline in the late 1940s (Fuchs 1982). A prime contemporary example would be the Brabant Island Expedition of 1984 sponsored by the British Antarctic Survey (Furse 1986, Moffat 1986). Over the course of a calendar year, biologists found both *Colobanthus quitensis* and *Deschampsia antarctica* not only growing but also flowering and setting seed, contrary to their initial expectations.

Taxonomy and biodiversity. One challenge facing botanists of the 20th century has been to comprehensively catalogue the biodiversity of the continent. To overcome this challenge, botanists first had to develop a concise taxonomy of the Antarctic flora (addressed earlier). The establishment of Antarctic scientific institutes and committees, along with advances in communication and transportation, allowed Antarctic botanists more easily to examine and compare specimens from different expeditions. Most notable in this respect is the 35-year-old Antarctic Plant Database of the B.A.S. (Peat 1998). This database not only contains herbarium records from all over the globe but also relays information on pertinent literary sources, taxonomic revisions, and G.P.S. data.

On the literary front, Skottsberg (1954) provided a manuscript on Antarctic angiosperms that was heavily cited for the remainder of the 20th century. In 1963 S. W. Greene and D. M. Greene published their "Check list of the sub-Antarctic and Antarctic vascular flora," which was also commonly employed as it ameliorated some of the discrepancies between collections and their nomenclature. The Antarctic Plant Database has also been critical in organizing taxonomy and biodiversity data.

Concerning the topic of species diversity, it is interesting to compare "current" species counts throughout the history of Antarctic botany (Table 3). As would be expected in all categories (except flowering plants), the number of recognized species has grown, if somewhat stochastically, since the first records. Researchers disagree as to the exact number of species in each group, but this is to be expected due to ambiguous definitions of species. Continued genetic studies in the upcoming century will help resolve, but probably not solve, the species debate in all groups. Furthermore, the recent recognition of Antarctica's endolithic microorganisms has added a new dimension to our concept of Antarctic biodiversity; genetic and molecular biological studies in these taxa are just emerging (De La Torre et al. 2003; Labrenz et al. 2005; Yi et al. 2005).

Phytogeography and ecology. Antarctic phytogeography was a major component of botanical research in the 1960s and 1970s; examples of works from this time period include R. E. Longton (1973), J. Pickard (1986), Pickard and R. D. Seppelt (1984), and A. Moffat (1986). Phytogeographic classification schemes continue to differ between modern researchers. Longton (1985) suggests that much of these differences arise from problems in species distribution and taxonomic data.

Since the 1970s, phytogeographic interests have expanded to include more ecologically-oriented research as well. Antarctic plants have been one focus of recent interests in

Table 3. Changes in Antarctic plant species counts over the 20th century as shown through selected references. Estimates are listed chronologically.

Author	Angiosperms	Lichens	Liverworts	Mosses
Brown (1928)	2	100+	–	50
Byrd (1935)	2	100	–	63
Rudolph (1966)	2	350+	6	<75
Longton (1984)	2	at least 200	25	85
Moffat (1986)	2	150	25	75
Seppelt (1986)	–	–	10	70
Hansom and Gordon (1998)	2	at least 200	–	85
British Antarctic Survey (2002)	2	300–400	~25	~100

global climate change trends: scientists are interested in how organisms from such cold environments will respond to altered habitat. Several papers have recently appeared on this topic (Doran et al. 2002; Kennedy 1995).

The potential role of Antarctic plants as bioindicators has recently been recognized. Native angiosperms may be able to attest to and predict climate change (Lewis-Smith 1994), and lichens and mosses may be useful as environmental indicators for toxic compounds (Bargagli et al. 1999; Poblet et al. 1997). Beyond their immediate utility, these measurements will help establish baseline data for comparison with future measurements and may provide empirical information on the effects of environmental context on element accumulation.

Studies of Antarctic species may provide answers to questions that initially arose from the study of non-Antarctic species. For example, investigators from Germany recently documented cyanobacteria species from the McMurdo Dry Valley Lakes that produced hepatotoxins similar to organisms from other climates (Hitzfeld et al. 2000). While the ecological and functional importance of these substances is still unclear, the observation that they are present in isolated Antarctic lakes may yield an important clue.

Plant introduction experiments. Plant introduction experiments (both accidental and deliberate) are a good model of how increased scientific understanding concerning the welfare of the continent has shaped subsequent scientific activity. Prior to the 1960s, there was a cavalier attitude toward the introduction or tolerance of foreign species on Antarctic soil. The previously-discussed plant introduction "experiments" of the Second British National Expedition (1909–1911) and the British Graham Land Expedition (1934–1937) are good examples. It is fortunate that, in most cases, the plants selected were so unfit for their environment that they posed no threat to the natural species. Beginning in the 1960s, we see a more conscientious approach to these experiments as they pertain to violating the continent. As the history of plant introduction experiments in Antarctica has been covered thoroughly by R. I. Lewis-Smith (1996), I will mention only some key events here.

In the summer of 1954–1955, F. D. Zenon transplanted two species of *Nothofagus* in soil from Tierra del Fuego to the western coast of the peninsula. Zenon's choice of plant was not likely accidental: the Swedish South Polar Expedition of 1901–1904 brought back fossil remains that were later identified as *Nothofagus*. A. Corte visited the site again in 1961 and found all specimens dead but did find *Poa pratensis* growing (Holdgate 1964). Recall that this grass was likely first identified by Lamb in 1944. Somehow (either through natural forces or once again through the actions of humans), *P. pratensis* had managed to move itself from Deception Island south to the peninsula. Thirty years later the grass was still growing at the same location (Lewis-Smith 1996), implying that this invasive species could potentially threaten the native flora. Zenon's experiment was doubly important because it showed that foreign spores and seeds could hitch a ride in transplanted soil and grow in Antarctic habitats. Along with his observations of *P. pratensis*, Corte also noted the remains of a fern and legume (Holdgate 1964).

Poa annua is a second invasive grass species that has managed to colonize portions of Antarctica (Skottsberg 1954). It was, in fact, the first non-native species that is documented as having survived more than one winter (Longton 1966, Deception Island).

Rudolph planted two strains of Kentucky bluegrass (*P. pratensis*) and *Diapensia ponica* in rock-cleared plots at Hallett Station during the summer of 1963–1964 (Rudolph 1966b). He concluded that soil nutrients were adequate and that temperature (but not light or moisture) was the key factor, emphasizing microclimate. Crucially, his results demonstrated that introduced plants were a plausible threat, and subsequently all specimens were destroyed at the conclusion of the experiment.

Bear in mind that, while scientifically informative, these studies have limited applicability, as they were often conducted with foreign soil and/or with foreign plants. The first transplantation experiment involving *Colobanthus quitensis* and *Deschampsia antarctica* was initiated by Young (1970) but regrettably was never followed up.

Physiology and reproduction. The tolerance of Antarctic flora to extreme conditions has fascinated scientists from the beginning, with recent interests turning to mechanisms of adaptation. Collins (1969) performed an exquisite study of plant response to volcanic activity on Deception Island, detailing the vegetation before and after activity and discussing the roles of ash, wind, precipitation, and plant habit on recolonization or regrowth. Notably, this was the first study that examined how volcanoes impacted a largely cryptogamic flora. On the continent, several American investigators showed that green algae survive the harsh conditions by adopting an endolithic lifestyle (Meyer et al. 1988; Ocampo-Friedmann et al. 1988).

Technical developments and accumulated knowledge have allowed botanists to take a biochemical-, chemical-, and molecular-level look at these adaptations (Ferrer et al. 2004; Salvucci et al. 2004; Schroeter and Scheidegger 1995; Tang and Vincent 1999; Xiong et al. 2000). Recent studies have also explored the dynamics of nutrient cycling within Antarctic ecosystems, where elements are often of limited supply and need to be utilized and recycled efficiently (Banerjee et al. 2000; Fernandez-Valiente et al. 2001). Cross-continental comparisons of physiologies of related organisms are now becoming possible and yielding new insights into how Antarctic organisms handle their environment (Pandey et al. 2004; Salvucci et al. 2004; Tang and Vincent 1999).

Potential impacts of higher levels of UV radiation on plants inhabiting some regions of the peninsula, due to the "ozone hole," have also intrigued researchers. A series of papers have recently been published describing the effects of UV-B on both *Colobanthus quitensis* and *Deschampsia antarctica* (Day et al. 2001; Ruhland and Day 2001; Xiong and Day 2001). Other researchers have looked at the roles of pigments in response to UV-B in *D. antarctica* (van de Staaij et al. 2002) as well as made evolutionarily-oriented comparisons of UV-protecting pigments across the botanical spectrum (Rozema et al. 2002).

Genetic studies. Though temperate and tropical plants have been the primary focus of genetics, which thrived in the second half of the 20th century, interests quickly turned to Antarctic plants as well. Some of the first genetic studies were chromosome studies conducted by both American (Young 1970) and Japanese (noted in Steere 1965) scientists. Chromosome numbers were found to be similar in polar and equatorial moss species. Isozyme and later gene sequence-based studies followed. A good example of this evolution begins with a study of isozyme variation for three different genera of mosses (Melick et al. 1994), wherein isozyme patterns were used to infer colonization events. The same research group followed this up with a study of randomly amplified polymorphic DNA (RAPD) markers in one species (Adam et al. 1997). Another commonly employed technique in genetics is the determination and comparison of internal transcribed spacer (ITS) regions in ribosomal DNA (rDNA). Romeike et al. (2002) utilized this technique to explore the genetic diversity in lichens from the Antarctic peninsula; besides characterizing the organisms' genetic diversity, the work produced important insights in regards to lichen colonization of Antarctica as well as symbiosis initiation. Genome sequencing projects, emerging in earnest in the 1990s, have just recently targeted polar organisms (Hoag 2003). Beyond phylogenetics, studies of Antarctic organisms are also teaching scientists about the nature and function of genes themselves (Odom et al. 2004).

Genetics is also helping us understand the historical importance of Antarctica (as a part of Gondwanaland) for plant dispersal. For example, Renner et al. (2000) studied chloroplast sequences of Atherospermataceae representatives to determine ancient Antarctica's importance in their current distributions. Genetic studies are helping us piece together not only the cyanobacterial family tree but also their relationships with microbes of adjacent McMurdo Lakes (Gordon et al. 2000).

Paleobotanical studies. The history of Antarctic paleobotany is a topic deserving an entire review unto itself and is much too robust to be treated in full here. Fortunately, a synthesis of our collective modern knowledge on the topic has been published (Taylor and Taylor 1992), which includes contributions from numerous researchers in the field as well as an exhaustive bibliography of all known papers and research notes prior to the publication date. I will note only a few critical and representative discoveries here.

While the Gondwanaland hypothesis had been validated by the middle of the 20th century, two key finds during this time increased our knowledge of *Glossopteris*. J. Mercer and J. Gunner located *Glossopteris* fossils of such quality that detailed histologic investigations could be made for the first time (Schopf 1970). A second find yielded the first *Glossopteris* fossils from the western side of the Transantarctic Mountains (the Pacific Ocean side of the continent) as well as the first pre-Triassic specimens (Craddock et al. 1965).

Finally, the first fossilized arbuscles (from mycorrhizae) ever discovered came from Antarctica towards the end of the 20th century (Stubblefield et al. 1987). These fossils were doubly important due to their implications for plant evolution as they suggested that symbiosis between plants and fungi may have contributed to the success and radiation of land plants.

Conclusion

I have endeavored to show the reader that Antarctic botany is worthy of biological, historical, and general scientific attention. At this point, the question naturally arises: How has this ("obscure" in many laypeople's eyes) scientific discipline managed to flourish? Not surprisingly, the factors contributing to Antarctic botany's growth and development have shifted over time.

The success of Antarctic sealing and whaling at the beginning of the 19th century was crucial to Antarctic botany's genesis. Economic, not political or scientific, motives drove early seafarers into Antarctic waters. Had these ventures not been fruitful financially, the birth of Antarctic botany would have been substantially delayed. So little was known of the continent that to speak of "Antarctic botany" as a distinct entity during this time period is perhaps misleading: botany was a small fraction of a nebulous "Antarctic science." In a strong sense, when botany took place, it was more the result of happenstance than deliberate intention. Whether Antarctica even *had* any vegetation to speak of was unknown by early naturalists such as Young. This changed with Hooker and his scientific work.

While financial motives continued to dictate the tempo of Antarctic exploration well into the 20th century, political and scientific incentives became fundamental influences starting in the mid- to late-1800s. Politically, explorers were driven to find and claim land for their countries. Scientifically, magnetic and oceanographic studies in Antarctica held broad, global consequences. Though not the focal point of any of these voyages, botany nonetheless prospered. We see scientists trying to fit their newly acquired and ever-multiplying knowledge of Antarctic flora into their understanding of botany as a whole, by comparing Arctic and Antarctic plants, as well as Antarctic island and mainland flora. Fossils added another dimension to the puzzle.

Indisputably, the most important factor contributing to the success of Antarctic botany in the early 20th century was its "Heroic Age." This period closely mirrored earlier ventures in the Arctic. Advertisement was key, with extensive campaigning and fundraising occurring prior to any expedition, and numerous public presentations or publications occurring subsequently. The influence of competition (both on individual and national scales) cannot be overlooked here: everyone wanted to be *the first* to explore sections of the continent, or to reach a landmark such as the South Pole. A striking change in the timbre of expedition journals occurred at this time: expedition leaders such as Nordenskjöld, Scott, Shackleton, and Mawson were proud of the accomplishments of all their men, scientific or otherwise, and discussed them all at length in their journals, which were oftentimes published. Antarctic botany benefited immensely and grew exponentially. "Doing botany" became a more deliberate action, as everyone now knew that there was botany to be done. Yet botany was still restricted mainly to exploration rather than science. Seldom was a hypothesis tested, or an experiment designed and executed (keep in mind that our "scientific method" of today is much different from that of the early 20th century).

In a very strong sense, the Heroic Age ended once the geographic and magnetic poles had been obtained. Antarctic botany would likely have languished in the ensuing void had something else not replaced it: war. Military bases were established, and they not only brought scientists to the continent (to conduct research both during and between wars) but also left facilities and infrastructure behind for subsequent use by science. The "motive" behind Antarctic exploration had by the 1950s changed identities several times, wearing the guises of economic, political, scientific, and military interests. Despite this, Antarctic botany continued to grow in a seemingly linear fashion, both in size and scope, adapting to but phased little by these social turnovers.

Science itself replaced the military emphasis beginning in the late 1950s and continuing till today, mainly in the form of the Antarctic Treaty and its legislative offspring. International communication and cooperation have been hallmarks of the current time period and have prevented conflicts concerning issues such as marine life or mineral resources from reaching perilous proportions. Antarctic botany has metamorphosed into a science of experiment versus exploration though the latter remains an essential component.

Naturally, shifting social forces have not been the sole driving force in the development of Antarctic botany. Technological advances have also been important, both on the continent itself and away. Better methods of communication have allowed more frequent and speedier conveyance of information. Faster, more reliable forms of transportation have changed the way in which we can reach and explore the continent, as well as move scientists and supplies. Medical advances, in addition to those of communication and transportation, have made Antarctic habitation and exploration safer.

Cornerstone to the growth of Antarctic botany has been the dedication and tenacity of both earlier and contemporary Antarctic explorers and scientists. Antarctica, a largely unknown continent surrounded by unpredictable iceberg-laden seas, would have presented a formidable challenge to early adventurers. Even after the outline of the continent had been determined, nothing was known of its interior—explorers had to prepare as best they could for what dangers the mysterious whiteness concealed. That Antarctica would eventually be "conquered," if not by these individuals then by others, is not in dispute; rather, historical appreciation comes from understanding that *they were the first*, despite being (by modern standards) ill-informed and woefully unprepared. How different would history have been had Scott and his companions abandoned their *Glossopteris* fossils? Or if Shackleton and his crew were deterred by the life-threatening ubiquitous crevasses and turned back? Nor should I neglect to mention the current Antarctic explorers who still face such formidable challenges.

Thus, a parade of widely varying (but linked) sociodynamic factors has parented Antarctic botany over the last 200 years. International scientific pursuits and cooperative legislation will likely continue to chaperone this science through the 21st century. Above all, Antarctic botany has taught us that accepted dogmas are constantly replaced with new data. We can therefore anticipate that the upcoming 200 years will bring equally exciting discoveries.

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Notes

1. The similarly named Adelaide Island, also at 66° south latitude but on the opposite side of the continent, was discovered in 1832, but its discoverer made no notes of its flora (Biscoe 1901).
2. A compilation of the geological finds from the entire expedition are considered in Appendix II of the expedition journal (David and Priestley in Shackleton 1909).
3. These specimens were cached, but when the party returned a year later (29 November 1913) to recover the specimens, so much snow had fallen that the cache could not be located.

4. Watts had originally wanted Cardot (of the British National Antarctic Expedition, 1901–1904) to examine the finds, but Cardot's country was being ravaged by World War I at the time, and Watts believed that Cardot's personal collection ("herbarium of rarities") had been pillaged.
5. An instructive, if somewhat peculiar, example of this change would be the meritorious **Expedition to Graham Land (1920–1922).** I include this expedition here rather than in the main text because of its individuality. Composed of only two young members, T. W. Bagshawe and Lester (at 19 and 20 years old), the expedition's objective was to "complete the map" along a portion of the peninsula. This can be read in a botanic as well as a geographic sense: on this voyage, science and cartography were of equal importance. Among other accomplishments, the two young men documented the growth of a grass at Andvard Bay, Danco Coast (likely *Deschampsia antarctica*), mosses at Shag Point, and lichens and mosses at Bryde Island (Bagshawe 1939). Importantly, they also mentioned that the Dominican gull (*Larus dominicanus*) used mosses and lichens, alongside other objects, in nest construction. This expedition is clearly not representative of the "average" campaign that was conducted in this time period, but it does illustrate the diversity of ventures that were now beginning to occur in the Antarctic. It also showed quite clearly that huge expeditions were not requisite for fruitful science.
6. Siple had also been a member of the First Byrd Antarctic Expedition as a 19-year-old representative of the Boy Scouts.
7. To understand the importance of this discovery, recall Hartwig's earlier (1869) comment of how far life was believed to extend in the Antarctic.
8. This is the same island on which Charcot made earlier observations.

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