

Acta Botanica Weberi

A JOURNAL OF BOTANICAL RESEARCH, THOUGHTS, THEORIES, HISTORY, AND PERSONALITIES

ABW NUMBER 1 – 2018

– ISSN 2561-9357 –

ISSUED AUGUST 2018

GLOBAL PLANT DISTRIBUTION AND CONTINENTAL DRIFT : TWO MOSS SPECIES

*William A. Weber and Linna Weber Müller-Wille **

ABSTRACT

Two calcareous mosses are discussed in an attempt to understand their extraordinary global distribution. Both are lowland and coastal species that, surprisingly, also occur rarely at high altitude. One has a far-flung distribution worldwide. The phytogeographical displacements of *Grimmia incrassicapsulis* and *Leptodon smithii* have likely taken place over many millennia as the continental plates moved, carrying these mosses to their present positions. Accompanying tectonic forces carried them from coastal areas to the mountains. The most likely period for such displacement to have started is the late Permian to early Triassic when Pangaea began to break apart.

It appears these mosses have remained virtually unchanged over time. Ideas are offered about how they may have escaped the pressures of natural selection. The theories mentioned are substantiated by Dr. Weber's personal field experiences collecting and observing mosses, along with their habitats, throughout the world.

Suggestions for further research are proposed.

* 'I' refers to William A. Weber and 'we' to both authors.

I. INTRODUCTION: PLANT GEOGRAPHY, CONTINENTAL DRIFT, AND LIVING MOSSES

Biohistorical plant geography has chiefly examined extant vascular plants or the fossil record with little attention given to non-vascular plant groups. Two remarkable bryophyte species in particular, *Leptodon smithii* (Hedwig) F. Weber & D. Mohr and *Grimmia incrassicapsulis* B. G. Bell, have fascinating distribution patterns. These remarkable species are probably living relics of the super-continent Pangaea. Their present distribution may be explained as resulting from tectonic processes associated with its breakup. The observations presented here are based on my personal studies of the genera *Leptodon* and *Grimmia*.

Plant geography seems to continue to be preoccupied with the idea that distribution of widely separated plant groups is the result of migration. Especially in North America, the Bering land bridge has been thought to support the geographical distribution of plants, particularly in the Rocky Mountain West. Nevertheless, certain species disjunctions (including these two species) have been the result of other means of dispersal, and have not resulted in evolutionary differentiation since at least the Cretaceous.

The geological discovery and elucidation of the earth's plate tectonics, also supported by fossil evidence, has confirmed Alfred Wegener's hypothesis of continental drift. Wegener first presented this hypothesis on January 6, 1912 in an oral contribution in Frankfurt at the second Annual Meeting of the Geologische Vereinigung, and published it in 1912 (Wegener 1966). This paper develops ample evidence that these mechanisms created the disjunct distributions of some contemporary plant groups and related genera. It also highlights species which have not undergone substantial evolutionary change.

In late December 1949, I sat with the audience at the annual meeting of the AAAS (American Association for the Advancement of Science) in New York City. Continental Drift was still a contested hypothesis. However, the noted South African geomorphologist, Lester Charles King (1907-1989), admitted that the botanists had demonstrated so many taxa whose distribution patterns demanded an explanation (notably the floras of West Africa and Brazil, where the continents nested neatly and their geology showed definite correlations). This phenomenon, he stated, demanded explanations from geologists (*cf.* King 1953). In retrospect, this, for me, was the beginning of the acceptance of continental movements.

Wegener's theory has now been long established with no doubts left at all. The concept of the existence of a great continent, Pangaea, including Gondwana, which broke apart and dispersed into what have become the modern continents, is no longer an hypothesis (Krill 2009-2014). Evidence for continental drift, as Wegener formulated it, was provided by fossils of vascular plants, especially those groups linking West Africa with Brazil (Wegener 1966). There are other floristic evidences, which have not been highly touted. One is the Tethyan element, which involves the eastern Mediterranean flora and the flora of the Western United States; and, of course, we have known for many years the connections between the Appalachian and the eastern Asian floras.

Our observations corroborate Wegener's ideas and provide an explanation for the wide disjunctions of *L. smithii* and *G. incrassicapsulis*.

This essay will depart from the traditional format of scientific essays. After the discussion of two species of mosses with extraordinary distributions and characters, we will talk a bit about the state of the science of bryology, illustrate the increased need for field and herbarium studies, suggest areas dear to my heart for further research and action, and present a brief narrative depicting the path that led me to the hypothesis presented here.

II. TWO LIVING MOSSES WITH PANGAEAN DISTRIBUTION

I have had personal experience in the field with two mosses, *Leptodon smithii* and *Grimmia incrasscapsulis*, which exhibit a distribution pattern indicating origins as early as Pangaeon times. The worldwide distribution of these species (see maps, p. 9) indicates extreme longevity and a nearly complete escape from the pressures of natural selection. In the Colorado Rocky Mountains the almost total absence of endemism supports our thesis that the mosses have not undergone evolution over innumerable millennia.

Leptodon smithii (Hedwig) F. Weber & D. Mohr

Leptodon is now treated as one of two or more genera in the Leptodontaceae; the second genus *Forstroemia* contains two species. Formerly it was placed in Neckeraceae and other families before finally landing in Leptodontaceae (FNA Vol. 28, p. 623).

Leptodon smithii is likely the only member of its genus, but note the discussion in Sotiaux *et al.* (2009) concerning a recently described alleged Corsican endemic which they admit “is deeply nested within *L. smithii*” (2009, p. 192).

The first discovery of *Leptodon smithii* in Colorado was by Patricia Nelson in 1971 when she was a graduate student studying the mosses of a foothill canyon west of Denver. This discovery represented the only known occurrence on the North American continent and, at an altitude of 1830 meters, it is an anomaly for the species (Nelson 1973, Weber & Wittmann 2007, and Stark 2014). A second collection at the same locality, to ensure that the first one was not based on an accidental herbarium specimen fragment from another continent, was discussed by Weber & Wittmann (2007, pp. 102-103).

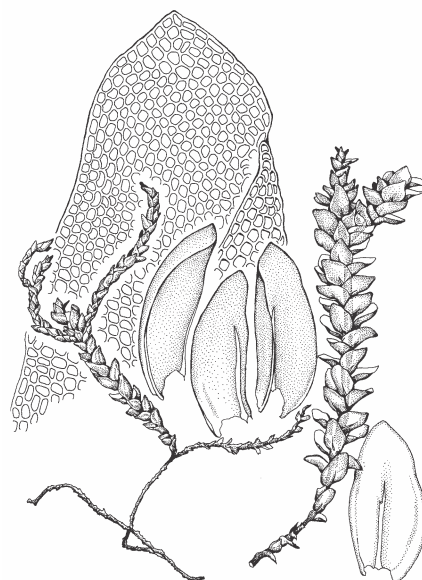
Until recently *Leptodon* was known in North America only from this single locality. While this paper was being prepared, a new locality was discovered in a nearby canyon and at a similar altitude by nine-year-old Spencer Smith and his father R. L. Smith. Their collection, a typical mature specimen, is deposited at COLO (R. L. & Spencer Smith 2015).

Description: *Leptodon* is a prostrate, branching, circinate pleurocarp in which the leaf-like phyllids of the lateral branches have a unique curvature, unlike the curvature seen in *Dicranum* or many aquatic mosses.

It was Johann Hedwig (1730-1799), the father of bryology, who first described this moss in 1801, naming it *Hypnum smithii*, after the famous James Edward Smith (1759-1828).

The type locality was “on tree trunks in Kent, near Barham Downs” (Hedwig 1801, p. 264) in the calcareous rock district of what is now County Kent, southeast England. It has always been a difficult genus to place very definitely in a family; it has been variously named over the centuries as *Alsia*, *Neckera*, *Orthotrichum*, *Pilotrichum*, *Pterigynandrum*, *Pterogonium*, and *Maschalocarpus*. Up until now *Leptodon* usually has been included in Neckeraceae.

The FNA treatment maintains Leptodontaceae, with three genera, and claims there are four species of *Leptodon*: *L. smithii* (Hedwig) F. Weber & D. Mohr, *L. corsicus* Enroth *et al.*, *L. longisetus* Montagne, and *L. pluvinii* (Brid.) A. Jaeger. However, the characterization of this family is not at all settled (Stark 2014).



Drawing: Patricia Eckel, from Weber & Wittmann 2007

Because this discussion is not concerned with the taxonomy and the status is still controversial, for purposes of this discussion I am treating *Leptodon* as a monotypic genus. It is worth noting that two of the three genera appear to have unusual distribution patterns that are the subject of this paper.

Distribution, substrate, and collections: In its evolutionary history we assume that there must have been other *Leptodon* species. *L. smithii* occurs on all the continents except Antarctica, but it is far from being cosmopolitan. As a distinct calciphile it is restricted to calcareous substrates, occurring on pure limestone, calcite inclusions in schist, and on the lower bark of trees that are coated with calcareous dust. In Greece I found it growing on the trunks of trees in limestone areas near the sea. Among specimens I have examined, the trees on which it is found are *Carpinus*, *Cassipourea*, *Castanea*, *Cupressus*, *Olea*, *Pinus*, *Podocarpus*, and *Quercus*. I collected it on limestone in New South Wales, Australia, France, Greece, and Colorado.

Though originally and essentially a coastal lowland species ranging from sea level to relatively low elevations, the rather high altitude occurrences of *L. smithii* in Colorado, East Africa and Réunion are exceptional.

Global distribution: As represented by specimens in the University of Colorado W. A. Weber Herbarium (COLO), the global distribution consists of many widely dispersed locations which in Pangaeian times were in somewhat closer proximity to one another and, crucially, were connected by a contiguous landmass. The list below comprises information taken from the herbarium labels giving (where known) location, altitude, year collected, and collector in italics.

Australia:

- Capital Territory, Booroomba Rocks, 30 km SSW of Canberra, 1979, *H. Streimann*;
- Capital Territory, Orroral Valley Lookout, Namadgi National Park, 34 km SW of Capital Hill, Canberra, 1350 msm, 1994, *H. Streimann*;
- New South Wales, Braidwood District, Budawang Range between Majors Creek and Araluen, 1967, *W.A. Weber & D. McVean*;
- New South Wales, Braidwood District, Budawang Range between Majors Creek and Araluen, 1967, *W.A. Weber & D. McVean*;
- New South Wales, Canberra region, Tinderry Mts., E of Michelago, west slope, along ridge between Tea Tree Creek and summit of The Twins, 900-1500 msm, 1967, *W.A. Weber & D. McVean*;
- New South Wales, Cooleman Plain, west side of Brindabella Range at Blue Water Hole, 1160 msm, 1967, *W.A. Weber & D. McVean*;
- New South Wales, Cooleman Plain, west side of Brindabella Mts., 1160 msm, 1967, *W.A. Weber & D. McVean*;
- New South Wales, Limestone Creek, 30 km NE of Cowra, 500 msm, 1992, *H. Streimann*;
- New South Wales, Mt. Wilson, Blue Mts. area, 1972, *W.B. Schofield*;
- New South Wales, Mt. Wilson, Blue Mts. area, 1972, *W.B. Schofield*;
- New South Wales, Oxley Road, 56 miles E of Walcha, 1968, *W.A. Weber & D. McVean*;
- New South Wales, Weeping Rocks, New England National Park, 72 km E of Armidale, 1400 msm, 1991, *H. Streimann*;
- New South Wales, Yarrangobilly Caves, 40 km NW of Adaminaby, 920 msm, 1979, *H. Streimann & J. Butler*;
- New South Wales, Yarrangobilly Caves, 1965, *D. McVean*;

Queensland, Bunya Mts. National Park, along trail from Burton's Well to Mt. Kiangarow, 1000-1200 msm, 1974, *D.H. Norris*.

Canary Islands:

Gran Canaria: just W of Cueva Corcho, 1340 msm, 1975, *P.L. Redfearn Jr. & M. Crosby*.

Chile:

Juan Fernandez, Isla Masatierra, Cumberland Bay Trail, 1972, *L. Landrum*;

Ñuble Province, between San Carlos and San Fabian, 1972, *C. Quierolo*;

Paraguas National Park, 1970, *L. Landrum*.

Crimea:

South Coast near Alupka. 1956, *A.S. Lazarenko & E.N. Lesnjak*;

England:

Devon, Torquay, Avenue Road, 1962, *C.C. Townsend*;

Minehead, Somerset, 1879, *Miss Gifford*.

France:

Alpes-Maritimes, La Roya torrent below Saorge, N of Breil, 1966, *W.A. Weber*;

Basses Pyrenées, Eaux-Chaudes, *E. Monguillon*;

Brittany, Cap Finistère, near Quimper, 1906, *C.A. Picquenard*;

Corsica, Corte, Forêt de Campotile, Tavimano Gorge, 1300 msm, 1905, *V. Schiffner*.

Haute Savoie, La Grande Gorge du Salève, S of Geneva, 1853, *M. Bernet*.

Herauld, Colobière-sur-Orb, 1913, *I. Douin*;

Nice, *A. Meyler*;

Pyrenées Orientales, *J.C. Schleicher*;

Pyrenées Orientales, Forêt Communale de Banyuls, c. 200 msm, 1969, *B.O. van Zanten & During*;

Pyrenées Orientales, Les Albères, Forêt de la Massane, 650-700 msm, 1969, *During & B.O. van Zanten*.

Georgia:

Gulripshi District, vicinity of Chernigovka village, 200 msm, 1985, *V. Vašák*.

Greece:

Crete, Lassithi Plateau, entrance of Dikteion Andron Cave, 1971, *W.A. Weber & P.W. Richards*;

Crete, Gorge of Samaria, between plateau of Omalos and Aghia Roumeli, 1971, *W.A. Weber & P.W. Richards*;

Kephalonia Island, Mt. Ainos region, 1200-1500 msm, m. Majo., *J. Bornmüller*.

Peloponnese, along the road about 0.5 km past Agia Triás towards Tripoli, c. 35 km E of Amaliás, 1981, *G. & P. Döbbeler*;

Peloponnese, Olympia, near the museum, 1971, *W.A. Weber & P.W. Richards*;

Peloponnese, Hill of Kronos, ancient Olympia, 1963 *C.C. Townsend*.

Hungary:

Heves County, Remete-Bérc Mt. near Mátrafüred, above the Csatornavölgy valley, c. 750 msm. 1951, *A. Boros*.

Italy:

Liguria, Val d'Andora by Alassio, on slopes between Stellanello and San Bartolomeo, 100-200 msm, 1958, *M. Steiner & U. Jendralski*;

Sardinia, vicinity of Iglesias and Monteponi, 1971, *K. Holmen*;

South Tirol, Sarnthal valley, N of Bozen, 1867, *S. Berggren*;

South Tirol, Sarnthal valley, N of Bozen, 1867, *S. Berggren*;
Tuscany, Florence, Boboli, 1868, *F. Kiaer*;
Tuscany, Florence, Medici Villa della Petraia, 1885, *C.E. Correns*;
Border region of Southern France and Italy, *W.P. Schimper*.

Kenya:

Mt. Kenya, near Sirimon Gate, 2650 msm, 1976, *S. Rojkowski*;
Mt. Kenya, Sirimon Track, 2600 msm, 1976, *S. Rojkowski*;
Oldoinyo National Park, 2270 msm, 1976, *S. Rojkowski*;
Oldoinyo National Park, 2270 msm, 1976, *S. Rojkowski*.

New Zealand:

North Island, Hawke's Bay, Taradale, Sugar Loaf, c. 150 msm, 1959, *B.O. van Zanten*;
South Island, Banks Peninsula, Kaituna Valley, on slope of Herbert Peak, c. 850 msm,
1973, *D.H. Vitt*;
South Island, Marlborough, Kalkoura, Wairere Stream, 1974, *J. Lewinsky*.

Portugal:

District of Lisbon. Sintra, in village, 1960, *F.J. Hermann*;
Mata de Busaco, c. 400 msm, *P. Allorge*.

Réunion:

Arrt. sous le Vent, along path up SW slopes of Cirque de Cilaos, above village of Cilaos,
23km SE of St. Denis, 1350-1700 msm, 1972, *R. Marshall & Carol A. Crosby*.

Russia:

Ciscaucasia, Krasnodar region, 1958, *I.I. Abramov*;
Sochi District, Agura Waterfalls, SE of Sochi, 350-400 msm, 1979, *V. Vašák*;
Sochi District, Czernomorskaya near Sochi, 1926, *E. Gordnowa*;
Sochi District, vicinity of Matsesta Baths, left bank Matsesta River, 100-200 msm, 1981,
V. Vašák;
Sochi District, vicinity of Matsesta village, left bank Matsesta River, 50-300 msm, 1982,
V. Vašák;
Sochi District, vicinity of Matsesta village, left bank Matsesta River, 100-250 msm, 1983,
V. Vašák;
Sochi District, vicinity of Moldovka village, Mzymta River valley, 50-200 msm, 1982, *V. Vašák*;
Sochi District, vicinity of Razdolie village, Matsesta River valley, 20-100 msm, 1982, *V. Vašák*.

Slovenia:

Gozd Panovec (Panowitz Forest) near Nova Gorica, 1904, *K. Loitlesberger*.

South Africa:

Cape Province, Bathurst Div., Brooklands Farm, c. 21 km SSW of Grahamstown, 450
msm, 1975, *D.K. Bailey & A.J. Guillermond*;
Cape Province, Prince Albert District, Swartberg, 1947, *T.P. Stokoe*.

Spain:

Gipuzkoa/Guipúzcoa Province, Sierra de Aralar, 400-800 msm, 1966, [Unknown Collector].

Tanzania:

Monduli Mountains, on N-facing slope at lower edge of the Monduli Forest Reserve,
2000-2150 msm, 1988, *T. Pócs & R. Ochyra*;
Ngorongoro Crater, at edge of the crater, 1967, *G. Een*;

Ngorongoro Crater, near Lemala Ranger's post, 2340 msm, 1989, T. Pócs & S. Chuwa.

Tunisia:

Oued Lil, 35 km N of Jendouba, 650 msm, 1971, P. Robinson.

Turkey:

Adana Province, Bahce District (N. Amanus), Dumanli Dag Haruniye, 1200 msm, 1957, Davis & Hedge;

Mugla Province, 2 km N of Lila, 630 msm, 1971, N. Ayedem, A.C. Crundwell, E. Nyholm.

Uganda:

Bufumbira County, Mt. Muhavura, north slope, 2500 msm, 1969, K.A. Lye;

Kyotera County, 4 km W of Katera, 1160 msm, 1972, K.A. Lye;

Kyotera County, 6 km W of Katera, 1160 msm, 1972, K.A. Lye;

USA:

Colorado, Jefferson County, Bear Creek Canyon, c. 3 miles W of Morrison, above Bear Creek, 1950 msm, 2015, R.L. Smith & S. Smith;

Colorado, Jefferson County, Clear Creek Canyon west of Golden; 7 miles W of the road fork on west edge of town; just W of Tunnel Number 2; 1830 msm, 1971, P. Nelson;

Colorado, Jefferson County, Clear Creek Canyon, 7 miles W of Golden, above Clear Creek at the W end of Tunnel Number 2, ca. 1900 msm, 1972. W.A. Weber & P. Nelson.

Grimmia incrassicapsulis B. G. Bell

In August 1968, under the auspices of the Australian University, I spent a month at its field station in Papua New Guinea on the slopes of Mount Wilhelm. On what I was told was the only clear, rainless day in several years, I walked to the summit (4509 meters) with my friend Ben O. van Zanten. We saw virtually no vegetation on the rocks of the summit except for two bryophytes, a species of *Marsupella* and a small *Grimmia*. In the absence of a published treatment of *Grimmia*, the collection was filed in the herbarium for decades awaiting identification until I sent it to my colleague Ryszard Ochyra, who recognized it and actually had collected the species in Tierra del Fuego. Subsequently the Ochyras and I published a thorough discussion of the species (Ochyra, Weber, & Bednarek-Ochyra 2010). In February 2011, I was about to take my daughter Heather to Antarctica when Ryszard Ochyra wrote to tell me that if I wanted to see the little *Grimmia*, I should be advised to take the chair lift at Ushuaia, Tierra del Fuego, where I would be sure to find it.

The epithet *incrassicapsulis* refers to the extremely thick cell walls of the capsule, which might inhibit spore dispersal and practically eliminate any interior material. It may be that the species does not reproduce by spores at all; the capsule is imbedded in the plant tuft and not reaching above it. We have no way of knowing whether spore dispersal is very low or indeed absent.

It is curious that, except for the one collection at 4509 meters on Mount Wilhelm, the few other sites are lower than 300 meters. The alpine occurrence indicates that the moss had to have been growing on these substrates during the whole time of the tectonic uplift.

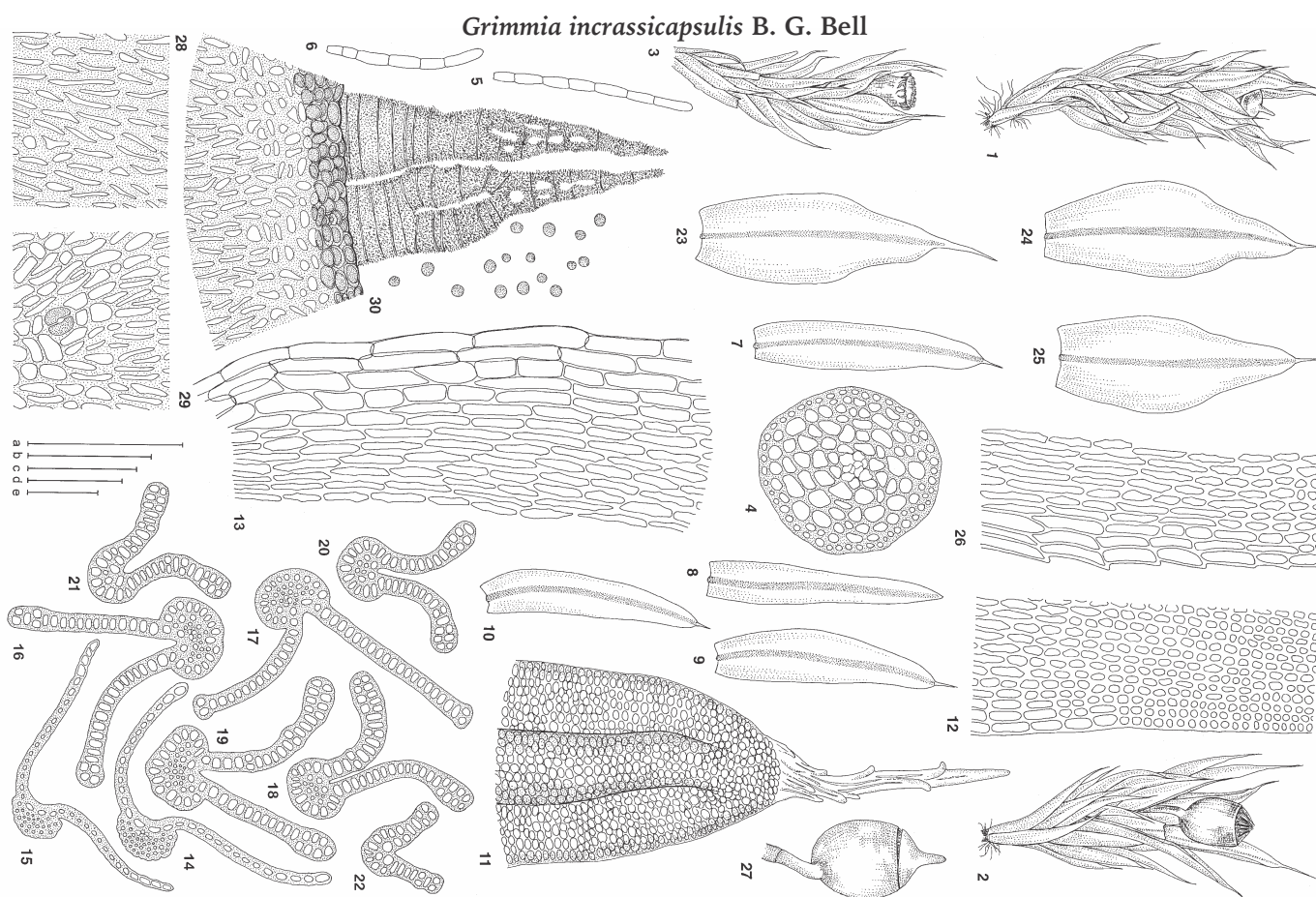
Fortunately, it has been adequately documented that the microhabitat for *Grimmia incrassicapsulis* is calcareous as Wade and McVean explain:



Drawing: Halina Bednarek-Ochyra
from Ochyra, Weber, & Bednarek-Ochyra 2010

“The summit ridges of Mount Wilhelm and Mt. Herbert, however, are composed mainly of gabbro [a plutonic rock consisting of calcic plagioclase and clinopyroxene] with more basic variants described as pyroxenite and hornblendite. Apatite is present as an accessory mineral in both the granodiorite and gabbro. The pyroxenite is extensively intergrown with magnetite, which forms considerable masses along the summit ridge, and the hornblendite is veined with epidote and calcite in places. McMillan and Malone (1960) suggest that the more basic rocks may predate the granodiorite which was probably intruded with epidote and calcite during the upper Triassic or lower Jurassic. The present form of the Bismarck Range seems to have been determined by folding and faulting during the Pliocene orogeny with some sculpture of the highest peaks by ice at a later stage.” (Wade & McVean 1969)

Global distribution: The known global distribution is discussed in Ochyra *et al.* (2010). The locations mentioned are in Papua New Guinea; Ushuaia and Isla Grande de Tierra del Fuego in Argentina; sub-antarctic South Georgia Island; and many sites in the alpine of New Zealand’s South Island. As with *Leptodon smithii*, the distribution of *Grimmia incrasscapsulis* displays a dichotomy in altitudes: all known localities are at or near sea level (cf. Greven 1995, 2003), except for that in Papua New Guinea at 4509 meters at the summit of Mount Wilhelm. Equally, *Grimmia*’s distribution has its origins in the same crucial contiguous landmass connection in Pangaeian times.

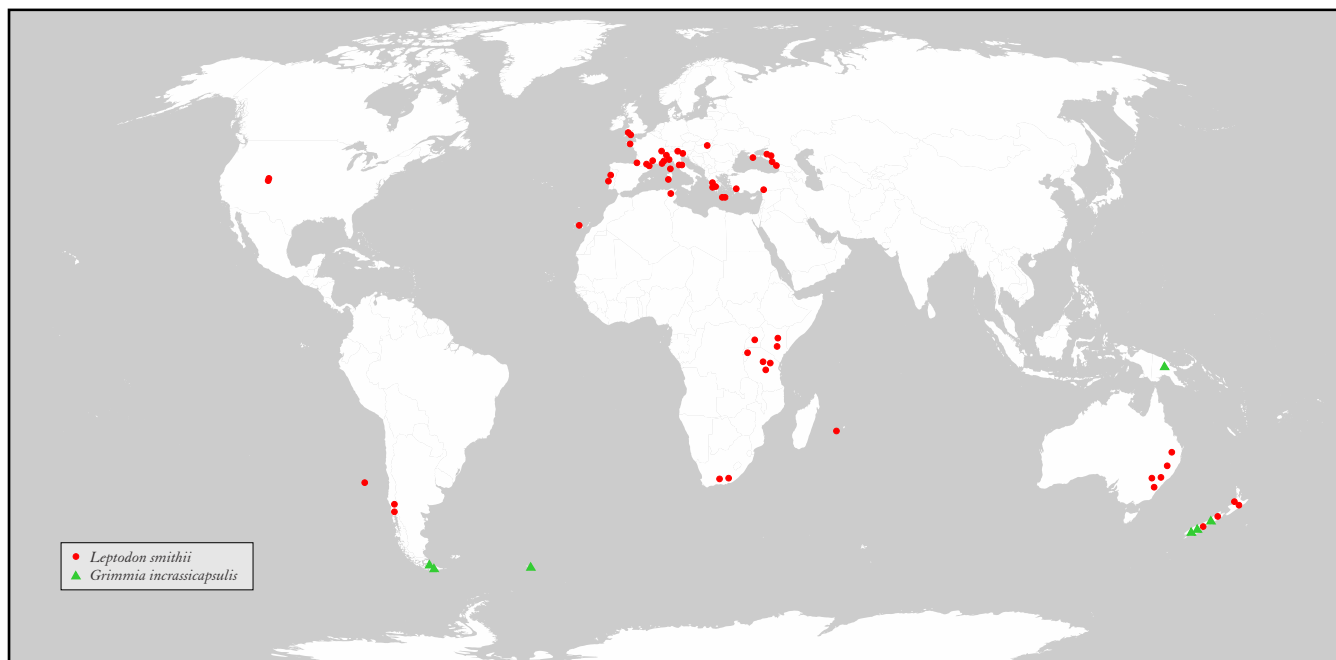


Drawing: Halina Bednarek-Ochyra, from Ochyra, Weber, & Bednarek-Ochyra 2010

© 2018 William A. Weber & Linna Weber Müller-Wille

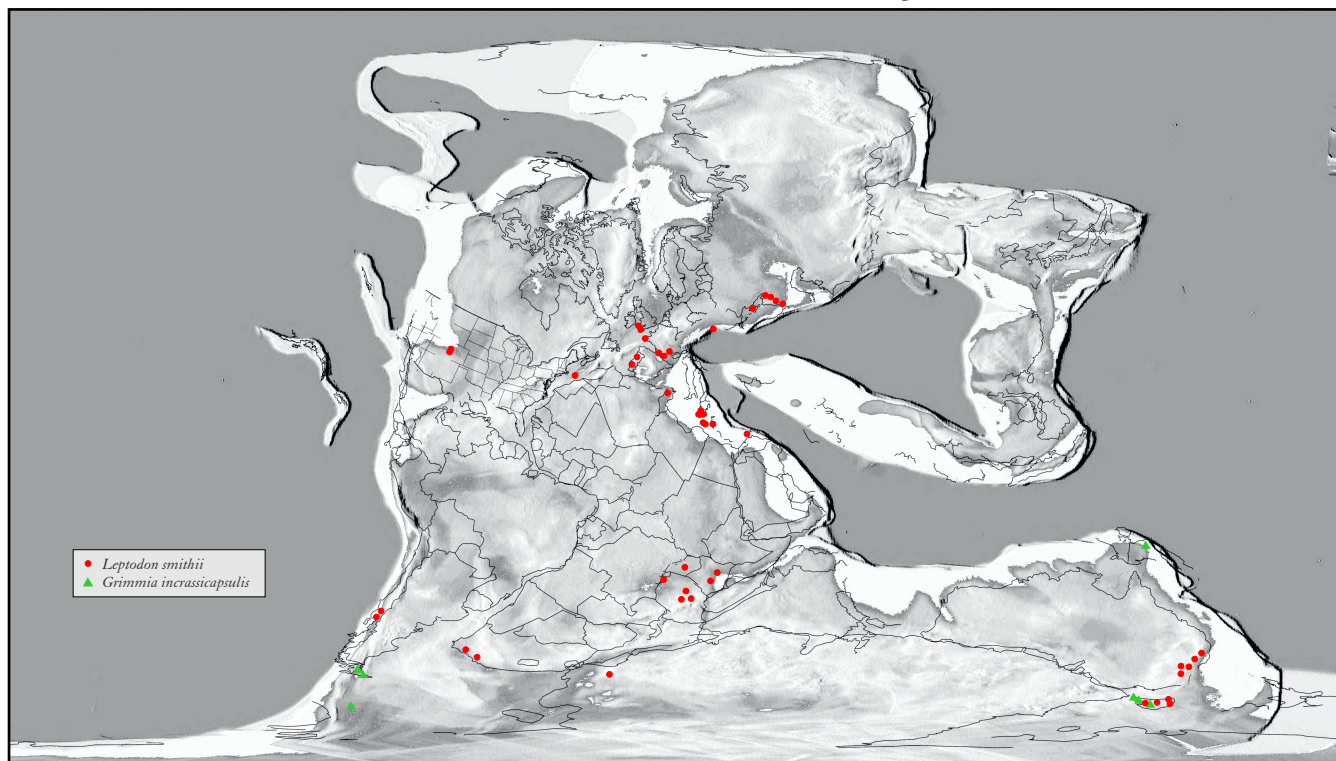
Global Distributions of *Leptodon smithii* (Hedwig) F. Weber & D. Mohr and *Grimmia incrasscapsulis* B. G. Bell

Known Present Day Localities as Represented in COLO



Map: Ragnar Müller-Wille using a base map from Free Vector Maps.com

Permo-Triassic (251 Ma) Positions of these Localities inferred through Continental Drift Calculations



Map: Ragnar Müller-Wille, using CR Scotese PALEOMAP Project, Map Folio 49 Permo-Triassic Boundary (251 Ma).

III. PHYTOGEOGRAPHY AND MOSSES

Disjunct Distributions: Though botanists have been well aware of disjunct distributions in the flowering plants, there has been little written about this phenomenon for the cryptogams, including mosses, especially in North America. Most of the patterns of plant geography, at least in the northern world, are still being explained by displacement via one or more vectors – birds, ocean currents, human migrations, and glacial expansion and contraction. Earlier, disjuncts were thought to be relicts of Tertiary populations. However, that idea did not explain the worldwide disjunct distributions of these plants.

I believe Alfred Wegener was on the right track in regard to flora with his continental drift ideas back in the early 20th century. The distributions we observe can easily be explained by continental movements.

George Gibbs' *Ghosts of Gondwana: The History of Life in New Zealand* (2006), a masterful elaboration, shows how biogeography on the world level is using molecular biology as its new tool. Historical phytogeography is neatly pictured by Gibbs as either *dispersal* across and beyond a barrier, followed by evolutionary differentiation of isolated populations, or as *vicariance*, in which a land mass splits apart, isolating two areas by way of a seaway or mountain system. Gibbs writes,

“... Vicariant species ... replace one another in space. Their current distributions, in isolation from each other, were brought about by the development of an inhospitable barrier between them, not by any migratory movement.” (Gibbs 2006, p. 46).

Hastings (2002) suggested that the distribution of *Grimmia teretinervis* is determined by the echo of the ancient Cretaceous seaway in Middle North America. He writes, “most of these sites are near the boundaries of ancient epicontinental seaways, particularly that of the Cretaceous”. Hastings (1999) previously had discussed the importance of habitat and the significance of the epicontinental seaway in determining the distribution of *Coscinodon*. *Orthotrichum hallii*, with a similar North American distribution (including Colorado), was reported from China (Lewinsky-Haapasaari & Tan 1995).

There is botanical evidence that a number of vascular plants also exhibit similar disjunctive patterns of distribution or vicariance.

During the decades leading to this essay, the Flora of North America project to produce complete treatments of the vascular plants and the bryophytes is making it possible, through the use of dot maps, to at least see the actual national distribution of all of the US flora. In Colorado, however, regardless of this boon, we have a flora for which these limited patterns are not sufficient.

The situation of the two bryophytes species discussed here illustrates the need for a worldwide program of standardized mapping techniques and representations adequately supported by the botanical institutions of the world.

Tectonics and mountain uplift: How did *Leptodon smithii* and *Grimmia incrasscapsulis* get to all of these places so widely separated by distance or altitude? The easiest answer would be, “The birds did it” or, “They locked up their little suitcases and marched thousands of miles” (the Bering Land Bridge is this kind of an answer). However, we now live in a new age, and know something about tectonics and continental movements.

I suggest we use the term *displacement* rather than migration, for that is actually what seems to have occurred as the continents drifted apart carrying species or populations with them. Plate tectonics also caused altitudinal displacement through mountain building, orogenesis, leaving some species at high altitudes and separated from their lowland counterparts. In *Ghosts of Gondwana*, George Gibbs gives convincing evidence that such distribution patterns originate from the breaking up of the ancient

continent of Pangaea, and are indicative of plate movement rather than migrations. The edge of the Colorado Front Range was once a seacoast 240 million years ago. Can it be that these mosses are as ancient as that?

Altitude and Distribution: The most striking characteristic shared by both *Leptodon smithii* and *Grimmia incrassicapsulis* is that their distribution patterns include isolated occurrences at much higher altitudes than are characteristic of the species elsewhere: the *Grimmia* at 4,509 meters altitude at the summit of the highest mountain in Papua New Guinea, and the *Leptodon* at 1,830 meters in a foothill canyon of Colorado in North America, at a similar altitude in Réunion, and in Kenya, Uganda, and Tanzania above 2,000 meters. This phenomenon very probably has not involved migration from lowlands to highlands, but rather was a spontaneous or synchronous movement of the population, a displacement by upheaval brought about by orogenic processes of mountain building as the continental plates moved. Keith Wade's observations in New Guinea suggest that this is what happened with *Grimmia incrassicapsulis* (Wade & McVean 1969). Hastings similarly concludes, writing about another species:

“... *Grimmia teretinervis* occupies calcareous limestones and sandstones that formed near the oceanic boundary and were subsequently uplifted by tectonic and thrusting events that created the Rocky Mountain Front Ranges.” (Hastings 2002, p. 264)

Many alpine mosses in the high mountains happen to be species that elsewhere occur in low coastal areas; in Colorado these simply became alpine as they were carried upward by tectonic movement. In the Rocky Mountains, at least, these coastal lowland species of mosses, lichens, and vascular plants are found at calcium-based alpine fens. A few examples among the vascular plants are *Phippisia*, *Koenigia*, *Hydrogrimmia*, *Armeria*, *Ptilagrostis*, *Primula egaliksensis*, *Eriogonum*, *Erysimum*, *Lesquerella*, and *Physaria*.

Among lichens, examples of these peculiar displaced distributions include:

Candelariella spraguei discussed by Bredkina (1982); and

Psora nipponica discussed by Timdal (1986), who worked with me in the field in Colorado on *Psora*.

Displaced mosses include:

Anoetangium handelii which occurs in Colorado, Nevada, Kurdistan, and Northern Iraq (Weber & Wittmann 2007, p. 120);

Didymodon anserinocapitatus found in Colorado, and western China (Weber & Wittmann, 2007, p. 124);

Leptodon smithii at altitude in Colorado, Kenya, Uganda, Tanzania and Réunion, elsewhere worldwide at low altitudes;

Grimmia incrassicapsulis on Mount Wilhelm in Papua New Guinea, Argentina, and the Subantarctic; and

Bryoxiphium norvegicum, a very rare species in a monotypic family; highly disjunct, occurring in Iceland, Greenland, Kamtchatka, Japan, American Midwest, Mexico, and at high altitude in Colorado and Mt. Rainier, Washington (Weber & Wittmann 2007, Löve & Löve 1953).

Evolution, Strategies, and Origins: We are confronted with some fascinating questions. How could a moss avoid evolving different species or being affected by natural selection while being isolated for so long

in so many widely separated localities? How can a moss species escape the changes that should be inevitable? There are some answers.

For a complete understanding of the life of a moss, read the excellent introduction in Seville Flowers' indispensable *Mosses: Utah and the West* (Flowers 1973).

1. The moss plant presents a haploid generation to the environment.
 - Being haploid, there is no possibility of the genotype carrying recessive genes that could permit the creation of new combinations should it be successful in an altered environment. This must be a powerful mechanism of escaping natural selection.
 - To succeed, it only requires a stable, if not wide ranging, microhabitat.
 - Longevity of the species is a matter of the haploid moss plant breaking into parts and starting more moss plants, without benefit of spores; simply breaking up when they are stepped on or otherwise abraded is all that it takes.
2. A great many mosses lack the ability to produce even an ephemeral diploid sporophyte; they succeed without sexual reproduction.
3. The cellular structure of the gametophyte is capable of resisting drying or wetting.
4. *Leptodon* is dioicous, meaning the plants are either male or female.
 - Female plants are rare and possibly non-existent; thus, there is no possibility of exchange of genes. The result is a breach of natural selection.
5. The moss plant can sustain its life indefinitely by a number of ways:
 - Many mosses have cellular devices, such as rhizoids, paraphyllia, pseudoparaphyllia, and gemmae. They may be like buds or leaf-like structures and can be distributed by breaking off the moss plant. Every living cell may give rise to buds and new shoots (Flowers 1973). The moss may propagate itself vegetatively through development of the bits and pieces that break off. So a moss can continue growing without benefit of any particular method other than fragmentation, and apparently may be able to survive and proliferate indefinitely.
6. Other features can further insulate a moss species from being destroyed in an environmental collapse.
 - Mosses can go into incredibly long periods of dormancy. My former student, Catherine LaFarge, recently revived a moss that had been rendered apparently lifeless under the glaciers of Ellesmere Island in the Canadian Arctic for 400 years (LaFarge *et al.* 2013). Not long after, a moss was revived after 1533-1697 years in the Antarctic permafrost (Roads *et al.* 2014).

Escaping the Pressures of Natural Selection: In the case of these two species it is simply speculation that drives us to the possibility that they do not reproduce sexually.

Leptodon smithii has escaped the pressures of natural selection in various ways, and has remained monotypic, probably since Pangaeian time. *Grimmia incrasscapsulis* has likewise evaded natural selection, but because there are so few collections, we know less about probable mechanisms for its success.

Features that may have to do with the success and invariability of these mosses over the ages may be the following:

- Restriction of habitat
- Calcium carbonate seems to be absolutely necessary for providing a habitat.

- The habitat falls into two categories of substrate containing calcium carbonate — the moss is equally abundant on the bark of tree trunks as on rock. It is especially common on dusty roads where presumably calcium carbonate is deposited with dust.
- Apparent lack of effective sexual reproduction: in *Leptodon*, sporophytes are extremely rare, and thus genetic diversity does not occur. Among the collections here at Colorado (81 specimens covering the entire world distribution) only one label indicates that the collector either saw or included a female plant, which had only a single partially decomposed sporophyte.
- *Leptodon* can be vegetatively reproduced by almost anything falling off the plant body, namely rhizoids, paraphyllia, gemmae, pseudoparaphyllia, and mere breakage of the stem or phyllids.
- It certainly is possible that the *Grimmia* may reproduce by fragmentation, but there are so few collections that we cannot be sure. It may be that the *Grimmia* does not reproduce by spores at all; the capsule is unusually dense and imbedded in the plant tuft. We have no way of knowing whether spore dispersal is very low or indeed absent.

Leptodon is usually abundant where it occurs, and evidently does not require the ability to penetrate its habitat, but simply to lie on it as a uniform population, unanchored with either soil or plant debris.

Important features of moss classification rest on the extraordinary, but probably relictual character of moss sporophytes. The future of bryology at this moment is guaranteed almost totally by the ability of mosses to reproduce by fragmentation of many sorts.

It is reasonable to assume that the occurrence of only one or a small number of stomates on the capsules is an indication that the stomates may no longer be functional. The extraordinary evolution of varieties of methods which prevented spore release must have occurred at some early period in moss evolution, in environments in which spores were profoundly necessary. We see the evidence of this early phase of the developments in the present mosses. We also should realize that the transformation of the strongly reduced sporophyte to a parasitic one on the gametophyte must have been an extraordinary leap in the early evolution of mosses, and is at this time absolutely without an answer.

We may have to enlarge our understanding that extreme longevity can occur without genetic change. The important features of moss classification rest on the extraordinary, probably relictual, character of moss sporophytes.

Summing up the various ways that the moss can avoid natural selection: The moss can endure unchanged over perhaps eons of time, and appears to be immune to environmental change. The ability to reproduce without throwing out new genes for testing makes it impossible for the environment to operate natural selection. However, if the moss is monoicous, it is possible for such a moss to be tested. In Colorado, for example, very few species produce capsules and spores; they just grow. In Australia after the big fires, the first things to come back are the mosses and liverworts – just like that! They're still there — unaffected by the environmental catastrophe.

All that is encapsulated simply in the statement that, with all of their structures, 99.9 percent of mosses are *not* affected by environmental pressure. Regarding those that are called subspecies, it is very doubtful whether these are really subspecies or simply environmental adaptations.

IV. RAMIFICATIONS

At this point it might be useful to recall the implications of the words from W. S. Gilbert and A. Sullivan's 'H.M.S. Pinafore' (1878), spoken by Buttercup:

*“Things are seldom what they seem,
Skim milk masquerades as cream,
Highlows pass as patent leathers,
Jackdaws strut in peacock’s feathers.”*
(No. 141 Duet (Captain Corcoran and Buttercup))

While this paper deals with only two extraordinary examples of possible origins, we observe that the gamut of species and genera of vascular plants, lichens, bryophytes—and probably everything else—consists of moving targets, exhibiting variations on this theme.

Origin of the alpine flora: In some of these genera and species the low altitude plant has disappeared, along with the habitat, leaving only the alpine derivative. This is further evidence that the alpine fens, such as those in South Park, Colorado, may be the last remnants of a seacoast flora in which calciphiles dominated. It is too early to speculate too much, but our eyes should be open to the possibilities of such local movement of formerly widespread entities. In most cases in America the lowland species are not present: *Armeria*, and *Phippsia*, and *Koenigia*, and all of those wonderful alpinines probably did not develop in the alpine zone, but on the shores. Considering the number of groups and species that are now alpine yet elsewhere in the world are coastal, it seems obvious that the origin of the alpine flora is the story of development of fens as orogenesis went on and the habitat adapted to high altitude.

Note on fens and bogs: In the Rocky mountains we may assume the fens originated as oceansides that were raised, bringing shore plants with them.

Fens are peatlands rich in minerals, fed by streams and groundwater. They reflect the chemistry of the underlying geologic formation. In limestone areas the water is rich in calcium carbonate, providing the alkalinity preferred by calciphiles. However fens are vulnerable to damage by drainage, or may acidify over time from runoff waters (especially in the vicinity of mines), becoming bogs. The calciphile species will then disappear. Changes in their characteristic plant assemblages are good indicators of environmental conditions.

Fens are extremely vulnerable habitats. It is essential to direct conservation initiatives to the protection of the alpine fens.

V. REFLECTIONS ON THE ‘WHAT’ AND THE ‘WHY’

From the 1940s to the 1980s in Boulder, I taught taxonomy mostly in the field and had to write my own textbooks for there were none then available. In 1946 I began building an herbarium at CU Boulder. The result of more than half a century of extensive fieldwork in Colorado and around the world, this collection (named the William A. Weber Collection in 2012) now contains more than 500,000 specimens and represents the most complete documentation of the flora of Colorado in the world. Evidence suggests that Colorado is not only an extraordinary place, but that it is one of the most exciting places in the realm of botanical origins! The William A. Weber Collection gives equal space to vascular plants, bryophytes, lichens, algae and fungi.

Since my official retirement from curator of the herbarium in 1986, I have been more and more intrigued by the bryophytes, little by little becoming aware of what they could tell us about historical phytogeography and evolution. Now, in 2018, after 85 years of taxonomy, dividing my studies among the vascular plants, lichens and bryophytes, I have finally begun to consider the puzzles of plant geography and origins in the light of evidence I have observed over nigh on a century. Just shy of my hundredth, after learning the “what”, I find that I am trying to understand the “why” — the origins of the floras. I am now seeing and pulling together threads in the “what” I have been observing that give me clues to an understanding of the “why” of these fascinating distributions.

How I got into phytogeography and this discovery

During World War II, as a conscientious objector I was sent to work at the Civilian Public Service camp at Cascade Locks, Oregon. The camp was beautifully situated in the Columbia River Gorge, and I have never been anywhere else in the world where there were so many mosses, everywhere! Awed and inspired, I spent my spare time exploring the gorges and collecting mosses and liverworts, which were abundant and unique. In the absence of any decent identification manual, I contacted the president of the Sullivant Moss Society, Henry Conard (1874-1971), to help me identify the difficult species. Conard (who at first mistook me for a forester!) was professor of botany at Grinnell College and was at the time the only person who knew the mosses. Thus began a long and fruitful dialogue between us. I had no idea then that I would eventually become Secretary-Treasurer, Vice-President, President, and curator-pro-tem of the Society's lichen herbarium, nor that fifty years later I would be returning the favor by helping out a young forester who contacted me for help identifying the moss flora of the same area!

In 1946, I became an instructor in biology at the University of Colorado in Boulder, and throughout my entire career I have continually been investigating the rich and diverse elements of Rocky Mountain phytogeography, and published many editions of what became a two volume flora of the vascular plants — *Colorado Flora* (Weber & Wittmann 2012).

In the early 1950s a colleague needed instructional material demonstrating the structure of a common lichen. Very few people in America could help me, but I was able to purchase a number of books, one of which was by A. H. Magnusson (1885-1964) on the analysis of the lichens collected by the expeditions of Sven Hedin (1865-1952) in Central Asia in 1927-35 (Magnussen 1944). I was able to match some of those accounts with specimens that I collected to begin to build a small lichen herbarium. One day in July of 1953, I was privileged to visit our alpine region with the renowned Norwegian lichenologist Eilif Dahl (1916-1993), who was a visiting professor at Colorado State College in Fort Collins. He taught me to recognize all of the common fruticose lichens, at the same time making me aware of Colorado/European connections in lichens and vascular plants.

In 1957, my interest was supported by a fellowship from the National Science Foundation, and I chose Stockholm, Sweden, to carry on my research. Using Stockholm as a base, I was able to visit the great lichen

herbaria of Uppsala, Lund, Copenhagen, and Bergen and borrow type material from several European museums. It happened to be a golden age in which I became well acquainted with the leaders in the field in Scandinavia: lichenologists Rolf Santesson (1916-2013), Gunnar Degelius (1903-1993), Ove Almborn (1914-1992), Hildur Krog (1922-2014), G. Einar Du Rietz (1895-1967), and A. H. Magnusson (1885-1964); plant geographers Eric Hultén (1894-1981) and Tyge W. Böcher (1909-1983), a Dane who co-authored the Flora of Greenland (1957, English translation 1968).

An instance of serendipity that pointed the way: I was walking in the botanical garden in Uppsala, Sweden, one morning in 1957 when Professor Nils Hylander (1904-1970), the curator, called me over, saying, “Some time ago you sent me a turf containing a special species, but that did not come up after the turf was planted. Instead I found that the plant that grew in its place was a *Sedum* very much like *S. semenovii*.” Then he showed me the plots where the two species were growing. Indeed, I failed to see any difference between them except that the Asian species was a little taller than ours. That *Sedum*, now called *Clementsia rhodantha* (A. Gray) Rose, is common along subalpine rivulets and fens in Colorado and is endemic in the Southern Rockies, but the similar *C. semenovii* (Regel & Herder) Borissova grows in the mountains of Asia and was discovered by Pyotr Semenov (1827-1914), the famous Russian explorer of the Tian Shan Mountains. This is an example of the close relationship between the Asian and Rocky Mountain floras (Weber 2003).

International Phytogeographical Excursions, 1961-1984: Over the years, I was invited several times to take part in the International Phytogeographical Excursions (IPE) of ecological taxonomic specialists. I participated in the IPE field trips to Finland and North Norway in 1961, the French and North Italian Alps in 1966, Greece and Crete in 1971, and finally to Japan in 1984. During my experiences in Sweden in 1957-58 and the IPE field trips, my eyes were opened to the phenomenon of wide disjunction, having seen in the field many species identical to those I knew from Colorado. These excursions allowed me to get to know the European botanists and learn the European flora in the field. It became obvious that to understand the flora of the Rocky Mountains it would be necessary to bring such people here to join me in the field. Over the years a great many of these foreign field botanists of all branches came to see the Rocky Mountains themselves.

The French IPE field trip in 1966 took us through the French and North Italian Alps to the classic area of the southwestern corner of France, visiting the collecting localities of William Nylander (1822-1899), the famous Finnish lichenologist, and I came home loaded with specimens. On a previous excursion to Finland and north Norway I met the Scottish field ecologist Donald N. McVean and helped him identify a number of rare lichens from Northern Scotland. The following year McVean contacted me from Australia where he had gone to work in the Australian alpine flora. He extended an invitation for me and my wife, Selma, to come to Australia for a year, 1967-68, with a stipend at the Australian National University at Canberra. Not only could I help Donald, but I could collect in all the most interesting areas, which included North Queensland, New South Wales, South Australia, Western Australia, and Tasmania, and make short trips to the Australian alpine Snowy Range (Weber 1969). Fortunately for me, Donald had a student, Keith Wade, who was working at a field station in Papua New Guinea in the subalpine at the foot of Mount Wilhelm, the highest point in that area. It was there that I encountered and collected an intriguing little moss, undescribed at the time. I saw that little *Grimmia* once again in Tierra del Fuego in 2011 when I was bound for Antarctica!

Looking toward the past and the future: vascular plants, lichens and bryophytes: Some time ago I published an essay on the history of boreal plant distributions that connect the floras of the Rocky

Mountains and the Russian Altai (2003). Joseph Dalton Hooker (1817-1911) discovered this connection 140 years ago. He knew the Middle Asiatic flora very well, and in 1877, traveling with Asa Gray (1810-1888) on a short continental tour, he spent five days in Colorado. He told about it in letters to Gray and Charles Darwin (1809-1882), and mentioned it as well in his memoirs. But, although he was the “father of plant geography” he never published on the subject. I should have been aware that “something was up” when I noticed a specimen collected by C. C. Parry (1823-1890) in Colorado had been identified by someone as “*Stipa mongolica*”!

As I review my career, I know that there are other patterns of distribution that need to be discussed more fully than before, but I realize I have no chance to live several more lifetimes. Therefore, I simply suggest a few projects occupying my mind that I would hope might be taken up by someone else.

VI. SUGGESTIONS FOR FUTURE RESEARCH AND DEVELOPMENT OF INTERNATIONAL RESEARCH TOOLS

- 1 **Calciphily:** We need to understand why calciphily occurs in plants in general, and mosses in particular. Calciferous substrates are not only the likely first land inhabited substrates, but for certain plants seem to be crucial to the survival of the species, for hitherto unknown reasons. Research into this phenomenon most likely requires international and interdisciplinary collaboration among botanists, geologists, chemists, and others.

- 2 **Global database:** A functioning worldwide cooperative and interactive database is a prerequisite for facilitating the exchange of information in respect to plant distribution, habitat, substrate, and many other field observations.

Many herbaria have carried on specimen exchanges with excicatti. It would be a tremendous boon to be able to use the internet as a centralized depository of documentation of such exchanges, both old and on-going. While this would be a huge undertaking, it is vital for our global understanding of phytogeographical and evolutionary problems as well as taxonomic issues. Modern technology, worldwide contacts among professionals, amateurs, and institutions make this a possibility.

Sadly, there is an attitude of parochialism about the larger collections. In an ongoing attempt to produce a database of specimen labels, only North American specimens are being selected, leaving the field without concrete information about world distributions.

In most collections, both historic and recent, labels generally lack data about substrate, exposure, altitude, and presence or absence of sporophytes. Bryologists, both professional and amateur, must develop an awareness of the importance of these data; they must train to recognize the diversity of these elements. With sufficient detailed data we will be in a position to be able to draw inferences and conclusions on many as yet unexplored aspects of historical plant geography on a global scale.

- 3 **Catalog of calcareous bryophytes:** Developing an interactive catalog of bryophytes that are limited to calcareous habitat is essential. Ideally, it would contain distribution and altitudinal collection data, location of voucher specimens, and collectors with contact information for those still with us. Such a catalog would be an invaluable research tool, and would go far to fulfill the dream of J. D. Hooker, the father of plant geography.
- 4 **Distribution mapping:** Standardization of requirements for the display of distributions maps will assure the most useful data. Most distribution maps are static entities with no real information that

can be used in a scientific way; most are merely dots or shaded areas and nothing more. They may pique our interest, but it is impossible to pursue inquiries based on the specimens represented on the map. This lack of data limits further research, making the maps essentially useless as a scientific tool.

Harold D. Harrington (1903–1981), in preparation for his *Manual of the Plants of Colorado* published in 1954, left a complete set of species maps on which he used dots to indicate the source from which an important collection was examined. Fortunately for our studies, his distribution dots that were special for any reason had an abbreviation for the herbarium where that specimen was seen and where that specimen could be found. This was before the days when herbaria had unique acronyms. It was a useful, if primitive, method of increasing the value of Colorado distribution maps.

Databases should be made on a global scope, rather than restricted to one country, as is usually the case. Such parochialism disregards a basic fact of plant sciences — plants have never recognized international borders. Maps and databases must be undertaken as international cooperative efforts, with standards set to ensure reliability and completeness of data for specimens represented across the globe.

With imaginative and innovative cartography it would be possible to design worldwide distribution maps with dots containing data such as substrate, herbarium, specimen location, type specimen, collector, and who identified the specimen. Certainly with digital methods this would be easily achieved.

Such a tool would enable us to uncover many patterns and to answer many questions. We may even find that bryophytes provide evidence that might be crucial in the search for origins of taxa.

- 5 **Conservation and protection of ecosystems:** We must find more effective means to protect ecosystems and conserve relictual habitats such as Mount Evans and Summit Lake.

Botanically, Colorado is probably the most important state in the US because of the distribution patterns which impinge on the North, South, East, and West, and because of the rich fossil record at Florissant, the Green River, and others. It has a number of famous national parks, but these were chosen for their esthetic values, rather than their ecosystems, which have developed and bear historical traces of activity since at least Cretaceous times.

The Mount Evans site had the promise of yielding important scientific information dealing with its various origins. Unfortunately, at the time, we did not realize the crucial significance of the lateral east-west connecting range, with its exciting alpine vegetation, extending from Mount Evans to Hoosier Pass and the Mosquito Range. The significance of such a lateral range was discussed in my Middle Asian paper (2003).

I was successful in 1965 in getting the US government to designate Summit Lake on Mount Evans as a scientific monument (Weber 1991). It appears in the National Register of Historic Places (NRHP), as a site deemed worthy of preservation. Summit Lake is likewise listed as a significant historic resource in the Colorado State Register of Historic Properties. However, these designations have no mechanism for protection of the ecosystem.

Some of the most important areas needing conservation have been ruthlessly affected: South Park has had the water of its rich calcicolous wetlands diverted to the populated areas east of the mountains; the highest areas have been provided with paved roads making them easily accessible and favorite goals for tourists; toxic mining spills in the San Juan Mountains have caused the rivers to run orange and go right through the sphagnum fens, changing their unique chemistry and plant assemblages. Ski areas, fires set by humans, uranium areas and drilling, introduction of exotic mountain goats as a tourist attraction, and many other activities are destroying these ecosystems. Efforts to protect individual endangered rare plants are unable to help restore an ecosystem.

Ecosystem protection and conservation requires interdisciplinary assessment of a defined area, with regard to a wide range of elements, including flora and fauna (both macro and micro), soil and water chemistry, risk of degradation by introduced flora and fauna, risk of damage by human activities, industrial and commercial activities, and many other factors. There needs to be a broad legislative approach for the preservation of such an area. It may be necessary to designate some areas off limits for all human and introduced activities. Such measures have long been implemented in other parts of the world: Finland has some national parks that are kept strictly inaccessible. Periodic interdisciplinary assessments to set benchmarks would be essential even for areas that seem not threatened. According to criteria established through interdisciplinary studies, a range of loose to highly restricted protections could be implemented into law.

Public education on the importance of ecosystems for the survival of the environment is a crucial part of the story. Interdependence in global human environmental relations must be stressed. Recreation, comfort, and entertainment must not continue to be our main priorities to the detriment of our planet's ecosystems.

- 6 **Continuing challenges:** Our speculations about the origins of bryophytes and lichens need verification and explanation of the how and why. In the light of new discoveries and analyses (i.e. Spribille *et al* 2016) made possible by new techniques, such goals seem to be within reach

Bryophyte taxonomy is mostly a concern of amateurs and the few professionals who have time to make identifications for them. Luckily, alongside the very few professional bryologists working in herbaria in North America, a strong wave of amateurs is increasing on the northeastern coast and in California.

We strongly suggest close collaboration among all interested in bryology, be they amateurs or professionals, sharing their knowledge and observations, along with application of cutting edge techniques. Such combined efforts may lead to new insights into the mysteries of origins.

REFERENCES

- Bredkina, L. I. 1982. Lichenes Montium Tian-Schan Centralis pro URSS novi. *Novit. Syst. PL. Non. Vasc.* 19:128-130.
- Gibbs, George 2006. *Ghosts of Gondwana: The History of Life in New Zealand*. Reprinted 2007, 2008; revised edition 2016. 232 pp. Craig Potton Publishing, Nelson, New Zealand.
- Harrington, H. D. 1954. *Manual of the Plants of Colorado*. 666 pp. Sage Books, Denver.
- Hastings, R. I. 1999. Taxonomy and biogeography of the genus *Coscinodon* in North America, including a new species. *The Bryologist* 102:265-286.
- Hastings, R. I. 2002. Biogeography of *Grimmia teretinervis* (Bryopsida, Grimmiaceae) in North America. *Bryologist* 105:262-266.
- Hastings, R. I., & H. C. Greven 2007. *Grimmia* Hedwig. In: *Flora of North America North of Mexico*, 27, Bryophyta, Part 1: 239.
- Hedwig, Joannis (Johannes) 1801. *Species muscorum frondosorum: descriptae et tabulis aeneis lxxvii coloratis illustratae*. Opus posthumum. 352 pp., 77 plates, ed. by Friderico Schwaegrichen J. A. Barth, Lipsiae (Leipzig).
- Flora of North America Editorial Committee, eds. 1993 ff. [FNA] *Flora of North America North of Mexico*. Vol. 1 ff. New York and Oxford.
- Flowers, Seville 1973. Ed. A. Holmgren. *Mosses: Utah and the West*. 567 pp. Brigham Young University Press, Provo, Utah.
- Greven, H. C. 1995. *Grimmia* Hedw. (Grimmiaceae, Musci) in Europe. 160 pp., figs, 32 color plates. Backhuys Publishers, Kerkwerve, The Netherlands.
- Greven, H. C. 2003. *Grimmias of the World*. 247 pp. (93 pages with line drawings, 1 map, CD-ROM with 160 species in color). Backhuys Publishers, Kerkwerve, The Netherlands.
- Ireland, R. R. 1982. *Grimmia teretinervis* (Musci, Grimmiaceae) in North America. *Bryologist* 85:332-334.
- King, Lester C. 1953. The Canons of Landscape Evolution. *Geological Society of America Bulletin* 64, 7:721-752.
- Krill, Allan 2009-2014. *Not getting the drift. A hard look at the early history of plate tectonics*. Trondheim. Open access by author. <http://folk.ntnu.no/krill/krilldrift.pdf>
- Krings, Michael & Thomas N. Taylor 2014. A fungal reproductive unit from the Lower Devonian Rhynie chert (Aberdeenshire, Scotland) that demonstrates an unusual hyphal investment pattern. *Scottish Journal of Geology* 51:131-139.
- Lafarge, Catherine, Krista H. Williams, & John H. England 2013. Regeneration of Little Ice Age bryophytes emerging from a polar glacier with implications of totipotency in extreme environments. *Proc. Natl. Acad. Sci. USA*. 110(24): 9839–9844. Published online 2013 May 28. www.pnas.org/doi/10.1073/pnas.1304199110.
<http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3683725/?report=classic>
- Lewinsky-Haapasaari, Jette & Benito C. Tan 1995. *Orthotrichum hallii* Sull. & Lesq. New to Asia. *Harvard Papers in Botany*, Vol. 1, No. 7, pp. 1-5. Harvard University Herbaria.
- Löve, A. & D. Löve 1953. Studies on *Bryoxiphium*. *Bryologist* 56:73-94; 183-203.
- Magnusson, A. H. 1944. *Lichens from Central Asia*, Part II. Pages 1-68. In: Reports from the scientific expeditions to the north-western provinces of China under the leadership of Dr. Sven Hedin (the Sino-Swedish expedition). 22, XI. Botany 2. Thule, Stockholm.
- McMillan, N. J. & E. J. Malone 1960. *The geology of the eastern Central Highlands of New Guinea*. 57 pp., map. Bureau of Mineral Resources, Geology and Geophysics. Report 48. Melbourne.

- Nelson, P. P. 1973. *Leptodon smithii* (Musci, Neckeraceae), a genus new to North America. *Bryologist* 76:434-437.
- Ochyra, R., W. A. Weber, & H. Bednarek-Ochyra 2010. Discovery of *Grimmia incrasscapsulis* (Grimmiaceae, Bryopsida) in Papua New Guinea. *Nova Hedwigia* 91:389-398.
- Roads, Esme, Royce E. Longton, & Peter Convey 2014. Millennial timescale regeneration in a moss from Antarctica. *Current Biology* 24,6.
- Scotese, C.R., 2013. Map Folio 49, Permo-Triassic Boundary (251 Ma), PALEOMAP PaleoAtlas for ArcGIS, volume 3, Triassic and Jurassic Paleogeographic, Paleoclimatic and Plate Tectonic Reconstructions, PALEOMAP Project, Evanston, IL.
- Smith, R. L. & Spenser 2015. Personal communication. Boulder, CO, November 15, 2015.
- Smith, S.J.E. 2004. *The Moss Flora of Britain and Ireland*. Second edition, 1026 pp. Cambridge University Press, Cambridge.
- Sotiaux, A. & J. Enroth, S. Olsson, D. Quandt, A. Vanderpoorten 2009. When morphology and molecules tell us different stories; a case-in-point with *Leptodon corsicus*, a new and endemic moss species from Corsica. *J. Bryology* 31:186-196.
- Spribille, T. & V. Tuovinen, P. Resl, D. Vanderpool, H. Wolinski, H. Stabentheiner, M. Toome-Heller, G. Thor, H. Mayrhofer, H. Johannesson, J.P. McCutcheon 2016. Basidiomycete yeasts in the cortex of ascomycete macrolichens. *Science* 353: 488-492
- Stark, L. R. 2014. Leptodontaceae Schimper. *Flora of North America north of Mexico*, 28, *Bryophyta*, Part 2: 623-628.
- Timdal, E. 1986 [1987]. A Revision of *Psora* in North America. *Bryologist* 89:253-275.
- Wade, L. K. & D. N. McVean 1969. *Mount Wilhelm Studies I. The alpine and subalpine vegetation*. Research School of Pacific Studies, Publ. BG/1. 225 pp. Australian National University, Canberra.
- Weber, W. A. 1940. *Potamogeton hillii* in Berkshire County, Massachusetts. *Rhodora* 42:95.
- Weber, W. A. 1965. Plant geography in the southern Rocky Mountains. [in] *The Quaternary of the United States*. H. E. Wright, Jr. & David G. Frey (eds.), pp. 453–468, Princeton University Press, Princeton, New Jersey.
- Weber, W. A. 1969. Of Shoes and Ships and Sealingwax. *International Lichenological Newsletter* 3, 1, June 1969:1-5.
- Weber, W. A. 1987. New names and combinations, principally in the Rocky Mountain Flora, VI. *Phytologia* 62:437–438.
- Weber, W. A. 1991. The Alpine Flora of Summit Lake, Mount Evans, Colorado. *Aquilegia* 15(4):3–10.
- Weber, W. A. 2003. The Middle Asiatic element in the Southern Rocky Mountain flora of the western United States: a critical biogeographical review. *J. Biogeography* 30:649-685.
- Weber, W. A., & R. C. Wittmann 1991. *Catalog of the Colorado Flora: A biodiversity Baseline*. University Press of Colorado, Boulder, CO.
- Weber, W. A., & R. C. Wittmann 2007. *Bryophytes of Colorado: Mosses, Liverworts, and Hornworts*. 231 pp., 8 plates. Pilgrims Process, Inc., Santa Fe, New Mexico.
- Weber, W. A., & R. C. Wittmann 2012. *Colorado Flora: Eastern Slope, A Field Guide to the Vascular Plants*. With the assistance of Linna Weber Müller-Wille. Fourth Edition. 555 pp., 104 line drawings, 1 map, 4 tables. University Press of Colorado, Boulder, CO.
- Wegener, Alfred 1966. *The Origin of Continents and Oceans*. Translated by John Biram from the 4th rev. [1922] German ed. Dover, New York, 246pp.

ABOUT THE AUTHORS

William A. Weber was born in New York City in 1918. He began to study bryophytes in 1933 when he was shown a small collection by his high school biology teacher, Grace Esternaux (born 1901), who had taken a bryology course at Cornell University. His first botanical paper was published in 1940 (see below). He has field bryological experience in the United States including Alaska and Hawaii, Canada, Mexico, Costa Rica, the Galapagos Islands, Canary Islands, Chile, Australia, Papua New Guinea, Europe, Nepal, and Russia. His most recent book on bryophytes was published in 2007 (Weber & Wittmann). His field investigations have taken him to many parts of the world and have included lichens, bryophytes, vascular plants, as well as phytogeography. His long-standing flora of Colorado (2012) culminated in a two volume work that included keys, phytogeographical and historical background material and stories from the field. He has published biographical works on Wilhelm Suksdorf, T.D.A. Cockerell, and C. C. Parry. He has a broad base as a character actor, choral singer, recorder player, and loves to sing Gilbert and Sullivan at the drop of a hat. He is a unique specimen.



Pertinent publications

1940. *Potamogeton hillii* in Berkshire County, Massachusetts. *Rhodora* 42:95.
2007. [with Ronald C. Wittmann]. *Bryophytes of Colorado: Mosses, Liverworts, and Hornworts*. Santa Fe: Pilgrims Process, Inc. 231 pp., 8 plates.
2012. [with Ronald C. Wittmann]. *Colorado Flora: Eastern Slope, A Field Guide to the Vascular Plants*. Fourth Edition. Boulder: University Press of Colorado, 555 pp., 104 line drawings, 1 map, 4 tables.
2012. [with Ronald C. Wittmann]. *Colorado Flora: Western Slope, A Field Guide to the Vascular Plants*. Fourth Edition. Boulder: University Press of Colorado. 532 pp., 108 line drawings, 1 map, 4 tables.

Biographical works

- T. D. A. Cockerell: A fifty-year project comprising four volumes documenting his life and works:
- *Theodore Dru Alison Cockerell, 1866-1948* (1966) [a bio-bibliography].
 - *Theodore D. A. Cockerell: Letters from West Cliff, Colorado, 1887–1889* (1976).
 - *The American Cockerell: A Naturalist's Life, 1860-1948* (2000).
 - *The Valley of the Second Sons: Letters from Theodore Dru Alison Cockerell written to his sweetheart and her brother about his life in West Cliff, Wet Mountain Valley, Colorado, 1887-1890*. (2004).
- C. C. Parry
- *King of Colorado Botany. Charles Christopher Parry, 1823–1890* (1997).
- Wilhelm N. Suksdorf:
- *The botanical collections of Wilhelm N. Suksdorf, 1850–1932*. Research Studies, State College of Washington 12, 1944:51–124.

Publications in plant geography

1962. Environmental modification and the taxonomy of the crustose lichens. *Svensk Botanisk Tidskrift* 56:293–333. 1 colored plate.
1965. Plant geography in the southern Rocky Mountains. [in] *The Quaternary of the United States*. H. E. Wright, Jr. & David G. Frey (eds.), pp. 453–468.
1966. Environmental modification in crustose lichens, II. Fruticose growth forms in *Aspicilia Aquilo*, Series Botanica 6:43–51.
1977. Environmental modification and lichen taxonomy. Chapter 2, pp. 9–29 [in] Seaward, M. R. D. (ed.), *Lichen Ecology*. Academic Press.
2003. The Middle Asiatic element in the Southern Rocky Mountain flora of the western United States: a critical biogeographical review. *J. Biogeography* 30:649–685.

Linna Weber Müller-Wille was born in 1942 in Colfax, Washington. She studied languages (German, French, Russian) aimed at scientific translations and geology and paleontology at the University of Colorado Boulder, the University of Helsinki, Finland, and the Westfälische Wilhelms-Universität, Münster, Germany. She and her husband Ludger Müller-Wille have cooperated in extensive anthropological and geographical projects with Sámi and Finns in northernmost Europe and with Dene and Inuit in northern Canada since the 1960s. She is a specialist in scientific translations and editing, especially arctic topics. She tagged along at her father's coattails her whole childhood, bringing him flowers, lichens, mosses, rocks, and other natural wonders. She helped in all aspects in the herbarium and in the field, collecting, pressing, mounting, drawing cells through the microscope, and alphabetizing Gray's index cards as soon as she learned to read. Recently, she assisted in the preparation and editing of the two-volume *Colorado Flora* (see above Weber & Wittmann 2012).



Photo: Ragnar Müller-Wille

Publications (translations and editing)

- *Saqqaq: An Inuit Hunting Community in the Modern World* by Jens Dahl. Toronto: University of Toronto Press, 2000, 277 pp.
- *Knowing Places: The Inuinait, Landscapes and the Environment (Les Inuit. Ce qu'ils savent du territoire)* by Béatrice Collignon. Circumpolar Research Series No. 10. Edmonton: Canadian Circumpolar Institute Press and University of Alberta Press, 2006. 304 pp.
- *The Sámi People, Traditions in Transition (Saamelaiset, Historia, yhteiskunta, taide)* by Veli-Pekka Lehtola. Inari: Kustannus Puntos 2002; second revised edition, Fairbanks: University of Alaska Press 2004. 137 pp.
- *Upheaval in the Arctic, Sámi in the Crossfire of War (Saamelainen evakko)* by Veli-Pekka Lehtola. (forthcoming).

Other publications

1969. Biometrical comparison of four populations of *Phoca hispida* Schreb. in the Baltic and White

- Seas and Lakes Ladoga and Saimaa. *Commentationes biologicae*, XXXI, 3. 12 pp. Helsinki: Societas scientiarum Fennica.
- 1974 and Ludger Müller-Wille. *Repulse Bay / Naujaa, N.W.T.* 1973. Saskatoon: (self-published). 27 pp., 24 photos. (Revised edition and German edition, Bonn, 1976)
1996. The North Calotte Library Conference Proceedings, Rovaniemi, August 16-18, 1995. *Arctic Centre Reports* 15. Rovaniemi: Arctic Centre, University of Lapland 1996. 65 pp.
- 2004 and Ludger Müller-Wille (eds.). Espaces – Lieux – Noms / Spaces – Places – Names. *Études/Inuit/Studies* 28 (2) : 5-131, 203-209.
- 2006 and Ludger Müller-Wille. Inuit Geographical Knowledge One Hundred Years Apart. In: *Critical Inuit Studies. An Anthology of Contemporary Arctic Ethnography*. Ed. by Pamela Stern and Lisa Stevenson. Lincoln and London: University of Nebraska Press, p. 217-229.

ACKNOWLEDGMENTS

Throughout my work as a botanist I have been very fortunate to have had the invitations and personal help of my numerous colleagues to aid me in my field studies in Europe, Russian Asia, Australia, Papua New Guinea, South America, North America, and Antarctica.

This paper evolved over the last few years in closest discussion and cooperation with my eldest daughter, Linna Weber Müller-Wille, and with additional editorial support by my son-in-law, Ludger Müller-Wille, grandson Ragnar Müller-Wille, granddaughter Heidi Alina, and great-granddaughter Chloé Gratton.

Acta Botanica Weberi

ISSN 2561-9357

<u>Publisher</u>	Ragnar Müller-Wille	<u>Editors</u>	Linna Weber Müller-Wille
	RMW Publications		Ragnar Müller-Wille
	Rawdon, Québec, Canada	<u>Copy Editor</u>	Heidi Alina
	rmw@williamaweber.com	<u>Website</u>	williamaweber.com

NOTE FROM THE EDITORS

Acta Botanica Weberi is published by members of the Weber family and distributed free of charge through the williamaweber.com website. It was specifically founded to publish this and other unpublished papers by William A. Weber. At the age of 99, Dr. Weber cannot wait on the peer review process to see his latest writings published if they are not to become posthumous works. Instead he and we feel that publication in this form to be the most appropriate at his age. The resulting dissemination of these works among his botanical colleagues, known and unknown, and the uses, references and discussions thus arising will be enough of a peer review and contribute to the continuing endeavors to research scientific questions.