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Comparison of the moss floras of Chile and New Zealand

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## A comparison of the moss floras of Chile and New Zealand Studies in austral temperate rain forest bryophytes 17

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**Summary:** Chile and New Zealand share a common stock of 181 species of mosses in 94 genera and 34 families. This number counts for 23.3% of the Chilean and 34.6% of the New Zealand moss flora. If only species with austral distribution are taken into account, the number is reduced to 113 species in common, which is 14.5% of the Chilean and 21.6% of the New Zealand moss flora. This correlation is interpreted in terms of long distance dispersal resp. the common phytogeographical background of both countries as parts of the palaoaustral floristic region and compared with disjunct moss floras of other continents as well as the presently available molecular data.

#### Introduction

Herzog (1926) called disjunctions the "most interesting problems in phytogeography and their explanation the greatest importance for genetic aspects". One of these interesting disjunctions is that between the southern part of Chile, New Zealand (and also southeastern Australia, Tasmania and southern Africa). Herzog (1926) wrote: "The strange fact that the southern part of South America south of 40° S lat. is an extraneous element as compared with the rest of South America and is more related to the remote flora of the SE-corner of Australia, Tasmania and New Zealand, allows to include these regions into an floristic realm of its own". Herzog called it the austral-antarctic floristic realm. Herzog (1926) made no attempts to explain the floristic similarity of these regions, although Wegener (1915) had published his continental drift theory already 11 years before the publication of Herzog's textbook. This theory was, however, not accepted by scientists and therefore not even discussed by Herzog but simply ignored. It took 50 more years until Wegener's theory was confirmed by the results of the studies on sea floor spreading and successfully used for the explanation of disjunctions of bryophytes.

Southern Chile and New Zealand share the same geological history: both were parts of the

Nothofagus province of the palaeoaustral region until about 82 mio years ago, at a time, when Africa had already separated from the former Gondwana continent (White 1990, Hill 1994). In contrast to other parts of this continent such as India, Antarctica or Australia, Chile and New Zealand remained since in a humid-temperate climate belt. Whereas in Australia the continental drift to the tropic of Capricorn revealed in an explosive speciation of dry adapted species, Chile and New Zealand preserved parts of the late cretaceous flora in their humid temperate forests. This concerns Nothofagus forest as well as ancient conifer forest, which consist of genera such as Agathis, Podocarpus, Libocedrus, Dacrvdium, Dacrycarpus, Fitzrova, Pilgerodendron among others. The floristic similarity between these former parts of the Gondwana continent, does, however, not only concern flowering plants but also bryophytes, which show much more affinities between Chile and New Zealand than flowering plants. The disjunctions in flowering plants are on a genus level, which demonstrates that even these ancient genera such as Nothofagus (Hill & Dettmann 1996) have evolved new species in these separate parts of the world. In contrast, bryophytes have a common stock of identical species. This raises the question whether the species identical in both parts are remnants of late cretaceous forests and have survived morphologically unchanged, or are identical because they have genetic exchange through the west-wind drift, which could disperse spores from New Zealand westwards over a distance of 10.000 km to Chile.

#### Comparison

A first estimation of the genera of bryophytes common in New Zealand and Chile was presented by van Balgooy (1960), who indicated 128 genera (=75%) as common to both regions. Seki (1973) in an evaluation of his collections in Patagonia indicated 14.7% of the mosses as circumsubantarctic (including S. Africa, Tasmania, Australia, New Guinea highlands, northern Andes and Central America). Van Zanten & Pócs (1981) calculated the relationship on the species level and indicated 122 species (=27%) in common. Matteri (1986) calculated the percentage of circumsubantarctic species from collections along a transect through Patagonia with 15.4%. An exact determination of the degree of conformity of the moss floras of New Zealand and Chile was so far really impossible due to the lack of checklists. However, in the past checklists of mosses were published by Fife (1995) for New Zealand and He (1998) for Chile, which provided the base for the present more exact comparison. At least, Beever (1999) gave an account of the similarities of the moss floras of Chile and New Zealand. Unfortunately, this interesting topic was published in a newsletter and thus got hardly recognition. According to her calculation, thirty-three percent of New Zealand's native moss species are recorded also for Chile. Our present calculation is based on species with an austral distribution, excluding not only introduced species but also species with a wider (cosmopolitan or subcosmopolitan) distribution.

The moss flora of Chile (He 1998) comprises 778 species and 88 subspecific taxa in 203 genera and 63 families. For New Zealand, Fife (1995) recorded 523 species and 23 varieties in 208 genera and 61 families. Both checklists were compared to identify the taxa identical in the floras of both regions.

#### Results

The comparison revealed that 181 species (+ 3 varieties) in 94 genera are identical in Chile and New Zealand (see tab. 1). The species common in Chile and New Zealand are listed in tab. 2. These are 23.3 % of the species and 63.1 % of the genera of the Chilean moss flora. It is, however, better to base the comparison on the moss flora of New Zealand, because Chile has also part of the neotropical flora. New Zealand shares 34.6 % of its species and of 61.5 % genera with Chile. If the species are excluded from this comparison, which are not confined to the austral region but are cosmopolitan or also occur e.g. in the tropical mountains or the holarctic (marked

with asterix in tab. 1), the number of species disjunct between Chile and New Zealand is reduced to 113, that are 21.6% of the New Zealand moss flora and 14.5% of the Chilean moss flora. If the mosses of Chile would be reduced to austral region and the neotropical species would not be taken into account, the percentage would probably as high as in New Zealand. On the genus level, Chile and New Zealand have 127 genera in common, which are 63% of the flora of Chile and 61% of the flora of New Zealand. Thirty-three of the 127 genera have no species in common.

The conformity is accordingly higher on the family level and concerns 76% of the genera of Chile and 78% of the genera of New Zealand.

The species in common belong to 34 families (tab. 3). Most of the species belong to the Bryaceae, followed by Dicranaceae, Pottiaceae, Orthotrichaceae and Amblystegiaceae.

#### Discussion

Bryophytes can absolutely not be compared with higher plants in terms of their phytogeography. In a most recent comparison of the flora of New Zealand and the southern Andes, Wardle et al. (2001) indicate the percentage of realm endemics of both parts with 90% of the species (465 species of the southern Andes and 522 of New Zealand) and 30% of the genera, however, only forty species or closely related pairs of species are shared. Half of the number of species is not identical but closely related, half of the rest belongs to the coastal vegetation, most of the remaining species are ferns and others (Deschampsia cespitosa, Trisetum spicatum) may ultimately be introduced from the northern hemisphere. It can therefore be generalized that higher plants of the austral realm are disjunct on a genus level, bryophytes on a species level.

The percentage of conformity of disjunct floras may be the result of long distance dispersal or relicts of a former closed range. A detailed discussion of this topic is given by van Zanten & Pócs (1981). It is still difficult to decide which factor is crucial. A molecular analysis can only state whether base sequences of certain genes of

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populations of the same species in disjunct populations are identical or not. Identical base sequences can, however, be the result of gene exchange but also of relict population, which have not undergone genetic changes since the separation of the populations (stenoevolution sensu Frey et al. 1999). Additional arguments are required to decide whether the species are able for long distance dispersal or not tolerance to frost or UV-radiation, see van Zanten (1976, 1978, 1983, 1984), sterility or rarety of sporulation, morphological arguments (spore size, cleistocarpy), habitats (epiphytes in the understory of forests as opposed to species from open habitats), life strategies (colonists vs. perennial stayers).

Nevertheless calculations of the degree of conformity of disjunct floras give an almost perfect correlation with the duration of separation (tab. 4) and not with the distance. If long distance dispersal would be the essential factor for explaining these disjunctions, tropical South America and tropical Africa would have more species in common than Chile and New Zealand, because both continents are closer than Chile and New Zealand. It could also be argued that tropical species are not as able for long distance dispersal as cool temperate species.

A further tool for differentiating relicts from species with gene exchange could be the interpretation of life strategies and habitats preferences. It could be argued that agressive colonists colonizing roadside banks (*Campylopus clavatus, C. introflexus*) are more likely dispersed by long distance dispersal than epiphytes in forests. About 30 species of the 187 common in Chile and New Zealand are epiphytic and therefore candidates for species with relict status.

Attempts have been made to solve the question experimentally (van Zanten 1976, 1978, 1983, 1984) and very recently by molecular studies (Meißner et al. 1998, Frey et al. 1999, Stech et al. 1999, Stech et al. in press, Pfeiffer 2000, Pfeiffer et al. 2000, Quandt et al. 2000, Quandt et al. 2001).

Van Zanten (1976) tested 139 disjunct bryophyte species for their ability for long distance dispersal

(germination experiments with wet- and dryfreezing). Amongst these species there were 38 species occurring in Chile and New Zealand. Sixty-six species did not germinate, with a considerable high percentage (67%) of diocious species. This might give an estimation of the percentage of species disjunct in Chile and New Zealand but with no genetic exchange. In contrast, only 23% of the 48 tested species occurring "closer" in New Zealand and Australia did not germinate. Of the 29 the species occurring in Chile and New Zealand und used in the germination tests (van Zanten 1978), most species were able to germinate after 1-3 years of desiccation. Only three species tolerated less than one year of desiccation: Weymouthia mollis and Fissidens rigidulus half a year and Lopidium concinnum only one month. Weymouthia and Lopidium are epiphytes, Fissidens is a hygrophyt. It has, however, to be kept in mind that these spore germination experiments were necessarily based on species which are producing sporophytes and a certain percentage of species is only known in sterile condition. Therefore the percentage of species with presumably no genetic exchange is in fact much higher than the results

The molecular studies were all made with the BRYOAUSTRAL-project using the *trn*L intron of cp DNA, which has proved to be most suitable for this purpose, with the following results:

of the germination experiments suggest.

# 1.*Hypopterygium* (Pfeiffer 2000, Stech et al. 1999).

*Hypopterygium*,,*rotulatum* "(Hedw.) Brid. from primary rain forests in New Zealand shows 100% sequence identity with *H. didictyon* from Chile. This disjunction is interpreted as palaeoaustral origin. Long distance dispersal is regarded as less likely because the species is dioiceous and has no vegetative reproduction. Even if the comparably small spores (10-17 $\mu$ m) are dispersed, a population cannot be established if not spores of both sexes land on the same spot. The existing stands are all bisexual. In addition it is difficult that this species growing on the floor of rain forests releases spores into higher air currents.

#### 2. Polytrichadelphus (Stech et al. in press)

Base sequences of *Polytrichadelphus* magellanicus from Chile and *P. innovans* from New Zealand show only small differences. Both taxa are therefore regarded as subspecies of *P.* magellanicus. The andine *P. longisetus* and *P.* umbrosus show a higher sequence variation and maybe derived from the latter. Genetic exchange can be excluded because the spores cannot tolerate dry or wet freezing (van Zanten 1978).

#### 3. Lopidium (Frey et al. 1999)

A comparison of populations of the epiphytic Hypopterygiaceae *Lopidium concinnum* from Chile and New Zealand showed no genetic differences. The relict status is supported by van Zanten's experiments (van Zanten 1978) which showed a desiccation tolerance of the spores of less than one month.

#### 4. Weymouthia (Quandt et al. 2001)

The sequences of *Weymouthia cochleariifolia* described from New Zealand and *W. billardieri* described from Chile show no differences. The closely related species *W. mollis* had a desiccation tolerance of spores of less than half a year (van Zanten 1978).

#### 5. Monoclea (Meißner et al. 1998).

*Monoclea gottschei* from South America and *M. forsteri* from New Zealand, two species morphologically very similar, have differences in base sequences on a species level (Meißner et al. 1998). This shows that both have originated from the same anchestor but have undergone a separate evolution after the separation of the populations. The evolution went on in South America, where *M. gottschei* ssp. *elongata* developed from ssp. *gottschei* by migration into the northern parts of the Andes.

In conclusion, the molecular data of species disjunct between Chile and New Zealand show three cases (see also tab. 5):

1. There are species with apparently no genetic interchange and no apparent evolution within the last 80 mio years (*Lopidium concinnum*,

*Weymouthia cochleariifolia, Hypopterygium didictyon*). Interestingly, the two first species concern epiphytes in rain forests.

2. There are subspecies derived from the same anchestor originated in Chile and New Zealand during 80 mio years with low molecular and morphological differences (*Polytrichadelphus magellanicus* ssp. *magellanicus* and ssp. *innovans*).

3. There are two species originated from the same anchestor (*Monoclea forsteri/gottschei*). Case two and three concerns epigaeic bryophytes.

Before the same geological background, the separation of the Gondwana continent, we can state bryophyte taxa with different rate of evolution within the same time span.

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percentage of conformity % taxa shared taxa Chile New Zealand Chile New Zealand total species 778 523 181 23.3 34.6 austral species 778 523 113 14.5 21.6 genera 203 208 127 63.1 61.5 families 63 61 76.2 78.7 48

**Tab. 1:** Comparison of the moss flora of Chile and New Zealand.

**Table 2:** Moss species common in Chile and New Zealand according to He (1998) and Fife (1995). The nomenclature has been homologized to He (1998). The list includes 181 species and three varieties. Questionable records *of Brachymenium exile, Bruchia hampeana, Bryum coronatum, Cyclodictyon sublimbatum* and *Ptychomnion aciculare* are included. Species marked with \* are not confined to the austral region but have wider ranges.

Achrophyllum dentatum Acrocladium auriculatum Amblystegium serpens \* Amblystegium varium \* Amphidium tortuosum Andreaea acutifolia Andreaea mutabilis Andreaea nitida Andreaea subulata Aulacomnium palustre \* Barbula calycina Barbula unguiculata\* Bartramia halleriana\* Blindia contecta Blindia magellanica Blindia robusta Brachythecium albicans\* Brachythecium paradoxum Brachythecium plumosum\* Brachythecium rutabulum \* Brachythecium subpilosum Breutelia elongata Breutelia pendula Breutelia robusta Bryoerythrophyllum jamesonii Bryum algovicum\* Bryum amblyodon\*. Bryum argenteum\* Bryum australe Brvum biliardieri Bryum caespiticium\* Bryum campylothecium Bryum capillare\* Bryum clavatum Bryum dichotomum Bryum laevigatum Bryum mucronatum Bryum muehlenbeckii\* Bryum pachytheca Bryum pallescens \* Bryum perlimbatum Bryum pseudotriquetrum\* Bryum rubens\*

Hookeriaceae Amblystegiaceae Amblystegiaceae Amblystegiaceae Orthotrichaceae Andreaeaceae Andreaeaceae Andreaeaceae Andreaeaceae Aulacomniaceae Pottiaceae Pottiaceae Bartramiaceae Seligeriaceae Seligeriaceae Seligeriaceae Brachytheciaceae Brachytheciaceae Brachytheciaceae Brachytheciaceae Brachytheciaceae Bartramiaceae Bartramiaceae Bartramiaceae Pottiaceae Bryaceae Bryaceae

Bryaceae

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Calliergidium austro-stramineum Calliergon stramineum\* Calliergonella cuspidata\* Calyptopogon mnioides Calyptrochaeta apiculata Calyptrochaeta flexicollis Camptochaete gracilis Campyliadelphus polygamum\* Campylopodium medium Campylopus acuminatus Campylopus clavatus Campylopus incrassatus Campylopus introflexus Campylopus purpureocaulis Campylopus pyriformis Campylopus vesticaulis Catagonium nitens ssp. nitens Ceratodon purpureus\* Ceratodon purpureus ssp. convolutus Chorisodontium aciphyllum Conostomum tetragonum Cratoneuron filicinum\* Cratoneuropsis relaxa Dendrocryphaea lechleri Dendroligotrichum dendroides Dicranella cardotii Dicranella jamesonii Dicranoloma billardieri Dicranoloma menziesii Dicranoloma robustum Dicranoweisia antarctica Didymodon australasiae Distichium capillaceum Distichophyllum krausei Distichophyllum rotundifolium Ditrichum austro-georgicum Ditrichum brotherusii Ditrichum cylindricarpum Ditrichum difficile Ditrichum strictum Drepanocladus aduncus\* Drepnocladus exannulatus\* Drepanocladus fluitans\* Drepanocladus uncinatus\* Encalypta rhaptocarpa\* Encalypta vulgaris \* Entosthodon laxus Fissidens adianthoides\* Fissidens asplenioides \* Fissidens curvatus

Amblystegiaceae Amblystegiaceae Amblystegiaceae Pottiaceae Hookeriaceae Hookeriaceae Lembophyllaceae Amblystegiaceae Dicranaceae Dicranaceae Dicranaceae Dicranaceae Dicranaceae Dicranaceae Dicranaceae Dicranaceae Phyllogoniaceae Ditrichaceae Ditrichaceae Dicranaceae Bartramiaceae Amblystegiaceae Amblystegiaceae Cryphaeaceae Polytrichaceae Dicranaceae Dicranaceae Dicranaceae Dicranaceae Dicranaceae Dicranaceae Pottiaceae Distichaceae Hookeriaceae Hookeriaceae Ditrichaceae Ditrichaceae Ditrichaceae Ditrichaceae Ditrichaceae Amblystegiaceae Amblystegiaceae Amblystegiaceae Amblystegiaceae Encalyptaceae Encalyptaceae Funariaceae Fissidentaceae Fissidentaceae Fissidentaceae

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Fissidens oblongifolius Fissidens rigidulus Fissidens serratus Fissidens taxifolius\* Funaria hygrometrica\* Glyphothecium sciuroides Goniobryum subbasilare Grimmia grisea Grimmia levigata\* Grimmia pulvinata\* Grimmia trichophylla\* Gymnostomum calcareum\* Hedwigidium integrifolium\* Hennediella arenae Hennediella heimii\* Hennediella serrulata Hymenostylium recurvirostrum\* Hypnum chrysogaster Hypnum cupressiforme Hedw. var. cupressiforme\* Hypnum cupressiforme var. filiforme\* Hypnum cupressiforme var. mossmanianum Hypnum revolutum\* Hypopterygium didctyon Isopterygium pulchellum\* Kiaeria pumila Kindbergia praelonga \* Leptobryum piriforme\* Leptodictyum riparium\* Leptodon smithii\* Leptotheca gaudichaudii Lepyrodon lagurus Lopidium concinnum Macromitrium longirostre Macromitrium microstomum Muelleriella angustifolia Muelleriella crassifolia Oligotrichum canaliculatum Orthodontium lineare Orthotrichum assimile Orthotrichum cupulatum\* Orthotrichum hortense Orthotrichum rupestre\* Papillaria flexicaulis Philonotis scabrifolia Plagiothecium denticulatum\* Plagiothecium lucidum Pohlia cruda\* Pohlia nutans\* Pohlia wahlenbergii\* Polytrichadelphus magellanicus

Fissidentaceae Fissidentaceae Fissidentaceae Fissidentaceae Funariaceae Ptychomniaceae Rhizogoniazeae Grimmiaceae Grimmiaceae Grimmiaceae Grimmiaceae Pottiaceae Hedwigiaceae Pottiaceae Pottiaceae Pottiaceae Pottiaceae Hypnaceae Hypnaceae Hypnaceae Hypnaceae Hypnaceae Hypopterygiaceae Plagiotheciaceae Dicranaceae Brachytheciaceae Bryaceae Amblystegiaceae Neckeraceae Aulacomniaceae Lepyrodontaceae Hypopterygiaceae Orthotrichaceae Orthotrichaceae Orthotrichaceae Orthotrichaceae Polytrichaceae **B**vaceae Orthotrichaceae Orthotrichaceae Orthotrichaceae Orthotrichaceae Meteoriaceae Bartramiaceae Plagiotheciaceae Plagiotheciaceae Bryaceae Bryaceae Bryaceae Polytrichaceae

Polytrichastrum alpinum\* Polytrichastrum longisetum\* Polytrichum juniperinum\* Pseudocrossidium crinitum Ptychomnion densifolium Pyrrhobryum mnioides Racomitrium crispipilum Racomitrium crispulum Racomitrium lanuginosum\* Racomitrium pruinosum Racomitrium ptychophyllum Rhacocarpus purpurascens\* Rhaphidorrhynchium amoenum Rhizogonium novae-hollandiae Rhynchostegium tenuifolium Sarmentvpnum sarmentosum\* Sauloma tenella Schistidium apocarpum \* Schistidium rivulare \* Sematophyllum uncinatum Sphagnum falcatulum Sphagnum subnitens \* Syntrichia andersonii Syntrichia papillosa \* Syntrichia princeps \* Svntrichia robusta Tetrodontium brownianum\* Thuidium furfurosum Thuidium sparsum Tortula atrovirens \* Tortula muralis\* Trichostomum brachydontium\* Ulota rufula Weissia controversa\* Weymouthia cochlearifolia Weymouthia mollis Zygodon gracillimus Zygodon hookeri Zygodon intermedius Zygodon menziesii Zygodon obtusifolius

Polytrichaceae Polytrichaceae Polytrichaceae Pottiaceae Ptychomniaceae Rhizogoniaceae Grimmiaceae Grimmiaceae Grimmiaceae Grimmiaceae Grimmiaceae Hedwigiaceae Sematophyllaceae Rhizogoniaceae Brachytheciaceae Amblystegiaceae Hookeriaceae Grimmiaceae Grimmiaceae Sematophyllaceae Sphagnaceae Sphagnaceae Pottiaceae Pottiaceae Pottiaceae Pottiaceae Tetraphidaceae Thuidiaceae Thuidiaceae Pottiaceae Pottiaceae Pottiaceae Orthotrichaceae Pottiaceae Meteoriaceae Meteoriaceae Orthotrichaceae Orthotrichaceae Orthotrichaceae Orthotrichaceae Orthotrichaceae

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Tab. 3: Number of species per families occurring disjunct in Chile and New Zealand.

Amblystegiaceae (14) Andreaeaceae (4) Aulacomniaceae (2) Bartramiaceae (5)	Lembophyllaceae (1) Lepyrodontaceae (1) Meteoriaceae (3) Neckeraceae (1)
Brachytheciaceae (7)	Orthotrichaceae (15)
Byaceae (23)	Phyllogoniaceae (1)
Cryphaeaceae (1)	Plagiotheciaceae (2)
Dicranaceae (20)	Polytrichaceae (6)
Ditrichaceae (4)	Pottiaceae (20)
Encalyptaceae (2)	Ptychomniaceae (2)
Fissidentaceae (7)	Rhizogoniaceae (3)
Funariaceae (2)	Seligeriaceae (3)
Grimmiaceae (11)	Sematophyllaceae (2)
Hedwigiaceae (2)	Sphagnaceae (2)
Hookeriaceae (6)	Tetraphidaceae (1)
Hypnaceae (6)	Thuidiaceae (2)
Hypopterygiaceae (2)	

**Tab. 4:** Degree of conformity of the mosses of various disjunct floras. The percentage is correlated with the time span of separation.

Disjunction	Percentage of species in common	Author	Age mio years
Europe – North America	70% of the species of North America	Frahm & Vitt (1991	) 50
Africa – South America	8% of the neotropical flora <sup>2</sup>	Delgadillo (1993)	180
Chile – New Zealand	33% of the species of New Zealand <sup>1</sup>	this paper 80	10.000 <sup>2</sup>

<sup>1</sup> The percentage is calculated on the flora of New Zealand because Chile is also part of the neotropical flora.

<sup>2</sup> The distance across the South Pacific Ocean is given, because it correlates with the prevailing wind systems.