

Distribution patterns in the genus *Peltigera* Willd.

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Abstract: The distribution of sixty-six *Peltigera* species in 230 biogeographic provinces or 40 regions are presented. A hierarchical clustering approach, used to identify clusters of species with similar distribution patterns (floristic elements), resolved four groups made up of Neotropical, Southern Hemisphere, Antarctic and mainly Holarctic species. The Holarctic Kingdom is species rich with the highest number of *Peltigera* species and also the highest number of endemic species; the Australian and Cape Kingdoms have the lowest number of species and endemics. The species rich provinces are briefly discussed.

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Key words: biogeographic provinces, lichens, *Peltigera* species, world distribution patterns.

Introduction

The world distribution of organisms has fascinated scientists curious about nature since early times (Brown & Lomolino 1998). However, studies analysing the geographical distribution of lichens are very scarce, especially compared with those that consider the distribution of angiosperms or pteridophytes. However, lichens have several characteristics that could provide valuable biogeographical information: they are considered to be ancient organisms (Lutzoni *et al.* 2001), their distribution can be easily and directly related to climate (Mies & Lösch 1995), and they display a great dispersal capacity, mostly due to the lightness of their spores and vegetative propagules (Kappen & Straka 1988; Mies & Lösch

1995). The scarcity of lichen biogeographical investigations is probably a consequence of the poor chorological knowledge of most lichen species.

Earlier papers dealing with lichen biogeography largely presented data in a subjective way and most of them present explanations based on inductive reasoning (Yoshimura 1968; Kurokawa 1972; Almborn 1985; Galloway 1988, 1991a,b, 1994; Jørgensen 1994; Moberg 1994; Goward & Ahti 1997; Cáceres *et al.* 2000; Otte *et al.* 2002). More recently Printzen & Lumbsch (2000) explored molecular variability to determine when and where *Biatora* and *Phyllospora* have diversified. Lücking (2003) undertook a comparative study of Takhtajan's floristic regions and foliicolous lichen biogeography and proposed six lichenogeographical regions.

Currently, phytogeographic studies in lichenology, as in other disciplines, are dependent on accurate taxonomic studies. The lichen genus *Peltigera* comprises 66 recognized species and includes terricolous and muscicolous foliose macrolichens, which are common and widespread on most continents. Although numerous taxonomic and

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TABLE 1. List of *Peltigera* species considered in the study, the presence of each species in the different Kingdoms and continents and main characteristics

| Species | Kingdom* | | | | | | | Continent† | | | | | | Summary‡ | | |
|---|----------|---|---|----|----|---|----|------------|---|----|----|----|-----|----------|-----|--|
| | H | N | P | AU | HL | C | NA | SA | E | AS | AF | AN | Prv | Reg | Suk | |
| <i>P. andensis</i> Vitik. | | + | | | | | | + | | | | | 2 | 1 | 1 | |
| <i>P. aphthosa</i> (L.) Willd. | + | | | | | | + | | + | + | | | 41 | 8 | 3 | |
| <i>P. aubertii</i> Dodge | | | | | + | | | + | | | | | 2 | 1 | 1 | |
| <i>P. austroamericana</i> Zahlbr. | + | + | | | + | | | | | | | | 10 | 6 | 5 | |
| <i>P. britannica</i> (Gyeln.) Holt.-Hartw. & Tønsberg | + | | | | | | + | | + | | | | 15 | 3 | 2 | |
| <i>P. canina</i> (L.) Willd. | + | + | + | + | + | + | + | + | + | + | + | + | 87 | 20 | 11 | |
| <i>P. chilensis</i> Gyeln. | | | | | + | | | + | | | | | 2 | 1 | 1 | |
| <i>P. chionophila</i> Goward & Goffinet | + | | | | | | + | | | | | | 6 | 2 | 1 | |
| <i>P. cichoracea</i> Jatta | | | + | | | | | | | + | + | | 3 | 3 | 2 | |
| <i>P. cinnamomea</i> Goward | + | | | | | | + | | | | | | 5 | 2 | 1 | |
| <i>P. collina</i> (Ach.) Schrad. | + | + | + | | + | | + | + | + | + | + | | 62 | 15 | 7 | |
| <i>P. continentalis</i> Vitik. | + | | | | | | | | | + | | | 6 | 3 | 2 | |
| <i>P. degenii</i> Gyeln. | + | | | + | + | | + | + | + | + | | | 42 | 9 | 5 | |
| <i>P. didactyla</i> (With.) J. R. Laundon | + | + | + | + | + | + | + | + | + | + | + | + | 87 | 26 | 11 | |
| <i>P. dilacerata</i> (Gyeln.) Gyeln. | + | | + | | | | | | | | | | 2 | 2 | 2 | |
| <i>P. dissecta</i> Purvis, P. James & Vitik. | + | | | | | | | | + | | | | 1 | 1 | 1 | |
| <i>P. dolichorhiza</i> (Nyl.) Nyl. | + | + | + | + | + | | | | | | | | 29 | 21 | 12 | |
| <i>P. dolichospora</i> Vitik. | + | | | | | | | | | + | | | 2 | 1 | 1 | |
| <i>P. elisabethae</i> Gyeln. | + | | | | | | + | | + | + | | | 45 | 8 | 3 | |
| <i>P. erioderma</i> Vain. | | | + | | | | | | | + | | + | 2 | 1 | 1 | |
| <i>P. evansiana</i> Gyeln. | + | | | | | | + | | | + | | | 11 | 5 | 2 | |
| <i>P. fibrilloides</i> (Gyeln.) Vitik. | | + | | | | | | + | | | | | 1 | 1 | 1 | |
| <i>P. friesiorum</i> Gyeln. | | + | | | + | | | + | | | | | 2 | 2 | 2 | |
| <i>P. frigida</i> R. Sant. | | | | | + | | | + | | | | | 1 | 1 | 1 | |
| <i>P. frippii</i> Holt.-Hartw. | + | | | | | | + | | + | + | | | 4 | 1 | 1 | |
| <i>P. horizontalis</i> (Huds.) Baumg. | + | | | | | | + | + | + | + | + | | 58 | 7 | 3 | |
| <i>P. hymenina</i> (Ach.) Delise | + | | | | | | + | + | + | + | + | | 28 | 4 | 2 | |
| <i>P. kristinssonii</i> Vitik. | + | | | | | | + | | + | + | | | 19 | 5 | 2 | |
| <i>P. laciniata</i> (G. Merr. ex Riddle) Gyeln. | | + | | | + | | | + | | | | | 9 | 5 | 3 | |
| <i>P. lairdii</i> Dodge & E.D. Rudolph | | | | + | | | | | | | | + | 1 | 1 | 1 | |
| <i>P. lambinonii</i> Goffinet | | | + | + | | | | | | | + | + | 2 | 2 | 2 | |
| <i>P. lepidophora</i> (Vain.) Bitter | + | | + | | + | | + | + | + | + | | + | 43 | 8 | 4 | |
| <i>P. leucophlebia</i> (Nyl.) Gyeln. | + | | | | | | + | + | + | | | | 53 | 8 | 3 | |
| <i>P. lyngei</i> Gyeln. | + | | | | | | | + | | | | | 2 | 1 | 1 | |
| <i>P. malacea</i> (Ach.) Funck | + | | | | | | + | + | + | | | | 49 | 9 | 3 | |
| <i>P. melanorrhiza</i> Purvis, P. James & Vitik. | + | | | | | | | + | | | | | 2 | 2 | 2 | |
| <i>P. membranacea</i> (Ach.) Nyl. | + | + | | | | | + | + | + | + | | | 58 | 11 | 5 | |
| <i>P. microdactyla</i> Nyl. | | + | | | | | | + | | | | | 1 | 1 | 1 | |
| <i>P. monticola</i> Vitik. | + | | | | | | + | + | + | | | | 16 | 5 | 3 | |
| <i>P. neckeri</i> Hepp ex Müll. Arg. | + | | | | + | | + | + | + | + | + | | 59 | 8 | 3 | |
| <i>P. neopolydactyla</i> (Gyeln.) Gyeln. | + | | | | | | + | + | + | | | | 38 | 7 | 3 | |
| <i>P. nigripunctata</i> Bitt. | + | | | | | | | | + | | | | 7 | 4 | 1 | |
| <i>P. occidentalis</i> (E. Dahl) H. Krist. | + | | | | | | + | + | + | | | | 6 | 2 | 1 | |
| <i>P. oceanica</i> Gyeln. | | | + | | | | | | | + | | | 2 | 1 | 1 | |
| <i>P. pacifica</i> Vitik. | + | | | | | | + | | | | | | 5 | 2 | 1 | |
| <i>P. patagonica</i> Räsänen | | | | | + | | | + | | | | | 2 | 1 | 1 | |
| <i>P. phyllidiosa</i> Goffinet & Miąlikowska | + | | | | | | + | | | | | | 3 | 1 | 1 | |
| <i>P. pindarensis</i> D. D. Awasthi & M. Joshi | + | | | | | | | | | + | | | 1 | 1 | 1 | |
| <i>P. polydactyloides</i> Nyl. | | | + | | | | | | | | + | | 3 | 2 | 1 | |
| <i>P. polydactylon</i> (Neck.) Hoffm. | + | + | + | + | + | + | + | + | + | + | + | + | 82 | 20 | 11 | |
| <i>P. ponojensis</i> Gyeln. | + | | | | | | + | + | + | | | | 46 | 6 | 3 | |
| <i>P. praetextata</i> (Flörke ex Sommerf.) Zopf | + | + | | | | | + | + | + | + | + | | 78 | 12 | 4 | |
| <i>P. pruinosa</i> (Gyeln.) Inumaru | + | | | | | | | | + | | | | 3 | 1 | 1 | |
| <i>P. pulverulenta</i> (Taylor) Nyl. | + | + | | | + | | + | + | | | | | 8 | 7 | 5 | |
| <i>P. retifoveata</i> Vitik. | + | | | | | | + | + | + | | | | 13 | 4 | 2 | |

TABLE 1 Continued.

| Species | Kingdom* | | | | | | | Continent† | | | | | | Summary‡ | | |
|---|----------|---|---|----|----|---|----|------------|---|----|----|----|-----|----------|-----|--|
| | H | N | P | AU | HL | C | NA | SA | E | AS | AF | AN | Prv | Reg | Suk | |
| <i>P. rufescens</i> (Weiss) Humb. | + | + | + | + | + | + | + | + | + | + | + | + | 89 | 20 | 9 | |
| <i>P. rufescentiformis</i> (Gyeln.) Dodge | | | + | | | | | | | | + | | 3 | 2 | 1 | |
| <i>P. scabrosa</i> Th. Fr. | + | | | | | | + | | + | + | | | 31 | 7 | 3 | |
| <i>P. scabrosella</i> Holt.-Hartw. | + | | | | | | + | | + | | | | 6 | 2 | 1 | |
| <i>P. soledians</i> Vitik. | | + | | | | | | + | | | | | 3 | 2 | 2 | |
| <i>P. spuriella</i> Vain. | | + | | | | | | + | | | | | 3 | 2 | 2 | |
| <i>P. subhorizontalis</i> Gyeln. | | | | + | + | | | | | | | + | 3 | 2 | 2 | |
| <i>P. truculenta</i> De Not. | | | | | + | | | + | | | + | | 3 | 2 | 2 | |
| <i>P. ulcerata</i> Müll. Arg. | + | + | + | + | + | + | | + | | + | + | + | 13 | 8 | 7 | |
| <i>P. vainioi</i> Gyeln. | | + | | | | | | + | | | | | 1 | 1 | 1 | |
| <i>P. venosa</i> (L.) Hoffm. | + | | | | | | + | | + | + | | | 46 | 8 | 3 | |

*H: Holarctic Kingdom; N: Neotropical Kingdom; P: Paleotropical Kingdom; AU: Australian Kingdom; HL: Holantarctic Kingdom; C: Cape Kingdom.

†NA: North America; SA: South America; E: Europe; AF: Africa; AS: Asia; AN: Australian-New Zealand.

‡Prv: number of provinces in which each species appears; Reg: number of regions in which each species appears; Suk: number of Subkingdoms in which each species appears.

chorological approaches have been conducted during recent years (Holtan-Hartwig 1993; Goffinet & Hastings 1994, 1995; Purvis & James 1993; Vitikainen 1985, 1986, 1994a,b, 1995, 1999; Goffinet *et al.* 1994; Goward *et al.* 1995; Goffinet & Miądlikowska 1999; Martínez 1999; Goward & Goffinet 2000), most of them were regionally based, so they lack the broad biogeographic perspective. However, Miądlikowska & Lutzoni (2000) carried out a phylogenetic revision of the genus based on morphological, chemical and molecular data. Despite these studies, knowledge of this genus remains geographically heterogeneous. The Northern Hemisphere is relatively well-studied and important collections are available in herbaria, except for central Asia, which remains poorly explored. On the other hand, the Southern Hemisphere is poorly known, although some studies are currently underway in the Neotropical (Vitikainen 1994b, 1995, 1999), Holantarctic and Australian Kingdoms (Vitikainen, in prep.). Nevertheless, *Peltigera* is one of the most extensively studied lichen genera, and so is a valuable subject by which to explore the distribution features of a widely distributed lichen genus.

The present study aims to identify the existence of groups of *Peltigera* species with significantly similar distribution patterns [floristic elements (Birks 1976)] in the world. In addition areas with the highest number of species are identified and discussed.

Materials and Methods

A. Data collection

Only well-accepted *Peltigera* species [e.g. see recent revisions by Vitikainen (1994a, 1999)] were included in the study and taxonomic categories below species were disregarded (Table 1). Recently, Miądlikowska & Lutzoni (2000) considered *Hydrothyria venosa* to be included in the genus *Peltigera*, as *P. hydrothyria* Miądlikowska & Lutzoni, but this species has not been included in this study because the data have already been analysed. Available data from the literature (more than 300 floristic papers) and from revised material from the most relevant herbaria for the genus (see Vitikainen 1994a) were compiled. The world was divided into 230 biogeographic provinces that mainly follow Tahktajan (1986), but with certain modifications from Quèzel (1978) for Northern Africa, and from Rivas-Martínez (1987, 1993) and Rivas-Martínez *et al.* (1999) for the Mediterranean Region and the American continent (Appendix 1). Classification of these units into higher levels follow Tahktajan (1986). Abundance of each species in a province was estimated with a five step linear scale based on the total number of records per species weighted by the size and the total number of

TABLE 2. Number of *Peltigera* species in each continent are indicated in the diagonal. Species shared between continents are indicated above and below the diagonal

| | Europe | Asia | N. America | S. America | Africa | Australia | N. Zealand |
|-------------|--------|------|------------|------------|--------|-----------|------------|
| Europe | 30 | 24 | 26 | 6 | 11 | 7 | 3 |
| Asia | 24 | 35 | 26 | 8 | 14 | 8 | 5 |
| N. America | 26 | 26 | 33 | 9 | 12 | 8 | 4 |
| S. America | 6 | 8 | 9 | 25 | 8 | 7 | 3 |
| Africa | 11 | 14 | 12 | 8 | 20 | 8 | 4 |
| Australia | 7 | 8 | 8 | 7 | 8 | 9 | 4 |
| New Zealand | 3 | 5 | 4 | 3 | 4 | 4 | 6 |

records per geographical unit. An abundance matrix (66 species \times 230 provinces) was prepared and subjected to further analyses.

B. Data analysis

The abundance matrix of species \times biogeographical provinces was submitted to a hierarchical clustering to classify species into homogeneous groups. Euclidean distance was used as distance coefficient and the UPGMA algorithm was approached to build a hierarchical classification. The optimal number of clusters or cut levels in the hierarchical classification was obtained by means of the cluster separation coefficient (Podani 1993). This coefficient was calculated for each level ('groups number'). The number of clusters in which the asymptotic value of the coefficient was first reached was considered the optimal classification structure. The number of clusters considered ranges between 2 and 10. Analyses were conducted with SYN-TAX v.4 (Podani 1993).

Results and Discussion

The presence of each of the 66 *Peltigera* species in the different Kingdoms and a summary of their distribution characteristics are presented in Table 1 and the number of *Peltigera* species found on each continent in Table 2. The number of *Peltigera* species on each continent in the Northern Hemisphere is rather similar (ranging between 30 and 35), whereas in the Southern Hemisphere this number decreases from 25 in South America to only 6 in New Zealand. Moreover, the three northern land masses share around 25 species, while the Southern Hemisphere barely reaches 10 species (Table 2).

The endemic *Peltigera* species in each continent are listed in Table 3. Species richness in the Holarctic reaches a maximum among the floristic Kingdoms (44 species with 30

endemics). The Australian (9 species with 1 endemic) and Cape Kingdoms (4 species and no endemics) are the poorest.

The Subkingdoms or equivalent geographical units with the highest number of species are the Boreal Subkingdom (40), Tethyan Subkingdom (31), Madrean Subkingdom (21), Andean Superregion (17) and African Subkingdom (14), the three former belonging to the Holarctic Kingdom. The regions with the highest number of *Peltigera* species are also situated in the Holarctic Kingdom: Circumboreal (35), Rocky Mountains and Iranian-Turanian (28), Eastern Asiatic (26), North American Atlantic (24) and Mediterranean (23). And finally, the provinces with the highest number of *Peltigera* species are also situated in the Holarctic Kingdom (Fig. 1).

Fig. 2 gives the optimal classification of species distributions produced by the hierarchical clustering analysis. The 66 *Peltigera* species were classified into four floristic elements; the most efficient partition being obtained at the four cluster level. At this step the separation coefficient reached the asymptotic level thus optimizing the differences among groups. The first group, namely group A, separates the Neotropical species and includes 3 subgroups. The second cluster (B) mostly separates very scarce species mainly distributed in the Southern Hemisphere and can be divided in 4 subgroups. The third group (C) separates Holantarctic species. Finally, the fourth cluster (D) includes most *Peltigera* species, mainly distributed in the Holarctic Kingdom and includes 7 subgroups (Fig. 2).

TABLE 3. Endemic *Peltigera* species in the different floristic Kingdoms. Total numbers of *Peltigera* species in each Kingdom are shown at the bottom of the Table

| Holarctic | Paleotropical | Neotropical | Australian | Holantarctic |
|--------------------------|----------------------------|------------------------|-------------------|-----------------------|
| <i>P. aphthosa</i> | <i>P. cichoracea</i> | <i>P. andensis</i> | <i>P. lairdii</i> | <i>P. aubertii</i> |
| <i>P. britannica</i> | <i>P. erioderma</i> | <i>P. fibrilloides</i> | | <i>P. chilensis</i> |
| <i>P. chionophila</i> | <i>P. lambinonii</i> | <i>P. microdactyla</i> | | <i>P. frigida</i> |
| <i>P. cinnamomea</i> | <i>P. oceanica</i> | <i>P. soledians</i> | | <i>P. patagonica</i> |
| <i>P. continentalis</i> | <i>P. polydactyloides</i> | <i>P. spuriella</i> | | <i>P. trunculenta</i> |
| <i>P. dissecta</i> | <i>P. rufescentiformis</i> | <i>P. vainioi</i> | | |
| <i>P. dolichospora</i> | | | | |
| <i>P. elisabethae</i> | | | | |
| <i>P. evansiana</i> | | | | |
| <i>P. frippii</i> | | | | |
| <i>P. horizontalis</i> | | | | |
| <i>P. hymenina</i> | | | | |
| <i>P. kristinssonii</i> | | | | |
| <i>P. leucophlebia</i> | | | | |
| <i>P. lyngei</i> | | | | |
| <i>P. malacea</i> | | | | |
| <i>P. melanorrhiza</i> | | | | |
| <i>P. monticola</i> | | | | |
| <i>P. neopolydactyla</i> | | | | |
| <i>P. nigripunctata</i> | | | | |
| <i>P. occidentalis</i> | | | | |
| <i>P. pacifica</i> | | | | |
| <i>P. phyllidiosa</i> | | | | |
| <i>P. pindarensis</i> | | | | |
| <i>P. ponojensis</i> | | | | |
| <i>P. pruinoso</i> | | | | |
| <i>P. retifoveata</i> | | | | |
| <i>P. scabrosa</i> | | | | |
| <i>P. scabrosella</i> | | | | |
| <i>P. venosa</i> | | | | |
| 44 | 15 | 18 | 9 | 18 |

Group A

This group separates 10 Neotropical species, which fall into three subgroups. However, due to imperfect knowledge of the taxonomy of Neotropical *Peltigera* species, discussion of these subgroups is fraught with ambiguities. The first two subgroups are represented by very scarce species, reported from only one to three biogeographic provinces.

The first subgroup comprises *Peltigera andensis*, *P. soledians*, *P. spuriella*, *P. fibrilloides*, *P. microdactyla* and *P. vainioi*, which are endemic species from the Neotropical Kingdom and distributed mainly in the Andean range. Almost all these species grow at high altitudes. As Schuster (1983) suggested in the case of Neotropical bryophytes, these high-elevation areas constitute

biotic islands that suffered the effects of Pleistocene glaciation. Rapid evolutionary processes coupled with such climatic change could explain the high levels of endemism. At least some of these taxa could be ancient but now have very restricted ranges (palaeoendemism).

The second subgroup is represented only by *P. friesiorum*, which is distributed in the Neotropical Kingdom and in the Tristan da Cunha Islands (Holantarctic Kingdom).

The third subgroup includes three species, reported from eight to ten biogeographic provinces and whose distribution areas are mainly spread in the Neotropical Kingdom, although they also grow in other Kingdoms. *Peltigera laciniata* is a Gondwana element, restricted to Central and South America (Neotropical and Holantarctic Kingdoms).

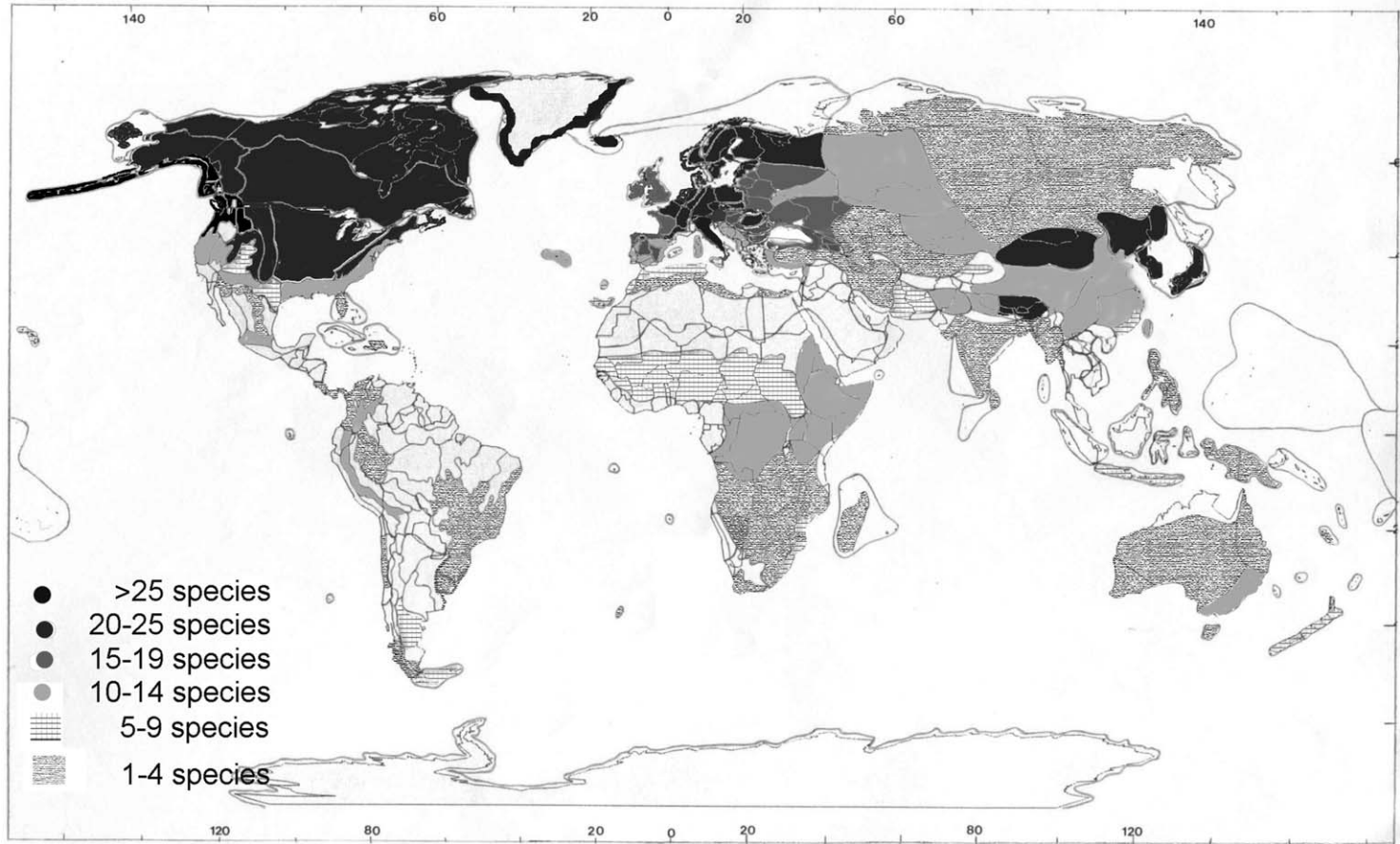


FIG. 1. World map showing the number of *Peltigera* species in the different biogeographic provinces.

Peltigera austroamericana and *P. pulverulenta*, which are known from South America (Neotropical and Holantarctic Kingdoms), and reach Central Mexico (Holarctic Kingdom), can be included in a North America-South American phytogeographical element (Qian 1999). They exemplify the significance of the current landbridge between North and South America which facilitates the biotic exchange between South and North American landmasses (Brown & Lomolino 1998).

Group B

This group, comprising 13 species, includes mainly very rare species distributed in the Southern Hemisphere. As in group A, different subgroups are apparent.

The *first subgroup* includes five endemic species from the Paleotropical Kingdom, although with very small, non-overlapping, ranges. *Peltigera cichoracea* is endemic to eastern Africa and Papua New Guinea, *P. polydactyloides* and *P. rufescentiformis* are endemic to central Africa, and *P. erioderma* and *P. oceanica* are endemic to the Indomalaysian Subkingdom (Philippinean and Papuan Provinces).

The *second subgroup* is formed by three species distributed in the Australian Kingdom. *Peltigera lairdii* appears only in the South-east Australian Province; *P. lambinonii* occurs in New South Wales of the Australian Kingdom and East Africa; and *P. dilacerata* is known from the Japanese-Korean and the South-east Australian Provinces.

The *third subgroup* is represented by two endemic species from Asia (Holarctic Kingdom). *Peltigera dolichospora* is endemic to central Asia (Northern Chinese and Eastern Himalayan Provinces) and *P. pruinosa* is an endemic of eastern and central Asia (Japanese-Korean, Taiwanese and Eastern Himalayan Provinces).

The *fourth subgroup* includes *P. dolichorhiza*, *P. ulcerata* and *P. subhorizontalis*. These species are distributed mainly in the Southern Hemisphere, but *P. dolichorhiza* and *P. ulcerata* are also found elsewhere. Thus, *P. ulcerata* grows in the Paleotropical,

Neotropical, Australian, Cape and Holantarctic Kingdoms, and is also present in the Holarctic Kingdom (only known from the Western Himalayan Province). *Peltigera dolichorhiza* is known from all floristic Kingdoms (except in the Cape). However, its presence in the Holarctic Kingdom is very limited, appearing only in the south of Mexico, the Himalaya range, Japan and Taiwan. On the other hand, the distribution area of *P. subhorizontalis* is restricted to Australia and New Zealand.

Group C

This group separates five very rare species known only from the Holantarctic Kingdom. *Peltigera aubertii* and *P. chilensis* are limited to the southernmost tip of South America (Argentina and Chile), *P. frigida* is restricted to Tristan da Cunha and Tierra del Fuego, *P. patagonica* is endemic to the Valdivian-Magellanic Region (Tierra del Fuego and Antarctic Provinces), and *P. truculenta* is restricted to the southernmost part of South America and to Marion and Prince Edward Islands.

Group D

This group separates a very large group of *Peltigera* species (38), which are exclusively or mainly distributed in the Holarctic Kingdom. Within this wide group, seven subgroups are recognized.

The *first subgroup* includes some rather abundant species, which are present in at least three different continents, and distributed mainly along circumpolar or circumboreal areas of the Holarctic Kingdom. These species are *P. aphthosa*, *P. neopolydactyla*, *P. elisabethae*, *P. degenii*, *P. leucophlebia*, *P. malacea*, *P. venosa*, *P. lepidophora*, *P. hymenina* and *P. scabrosa*. All of them are distributed in North America, Europe and Asia, except *P. hymenina*, which is known from North America, Europe and Africa (Macaronesian area), and *P. lepidophora* appears also in the Neotropical (South America), Paleotropical (Hawaii) and the Holantarctic (New Zealand) Kingdoms.

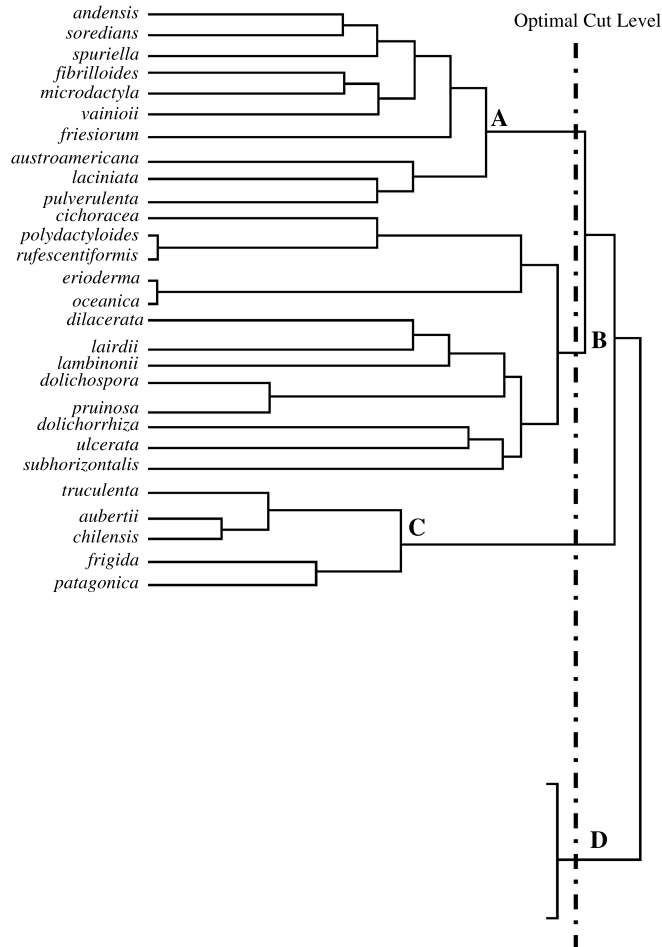


FIG. 2. Dendrogram of the floristic elements. A, B, C, D represent the four floristic elements.

The *second subgroup* includes five species, which are almost cosmopolitan and the most common species in the world: *Peltigera canina*, *P. didactyla*, *P. polydactylon*, *P. praetextata* and *P. rufescens*.

The *third subgroup* is also composed of five species: *P. collina*, *P. horizontalis*, *P. membranacea*, *P. neckeri* and *P. ponojensis*. The first three have suboceanic preferences, avoiding extreme continental situations. All of the species are distributed in the Holarctic Kingdom, but four of them have reached other Kingdoms. Thus, *P. collina* is found in some areas of the Neotropical (Mexico and Peru), Paleotropical (India), and

Holantarctic Kingdoms (Patagonia and Tierra del Fuego), *P. neckeri* is found in the Holantarctic Kingdom (Argentina and Chile), and *P. membranacea* reaches the south-west of India (Paleotropical Kingdom).

The *fourth subgroup* includes six species, these being the rarest Holarctic species and distributed mainly in Europe, although they are also present on other continents. *Peltigera britannica* is known from north-western and western Europe and from north-western North America. This disjunct distribution might not be surprising, because the climate conditions of western

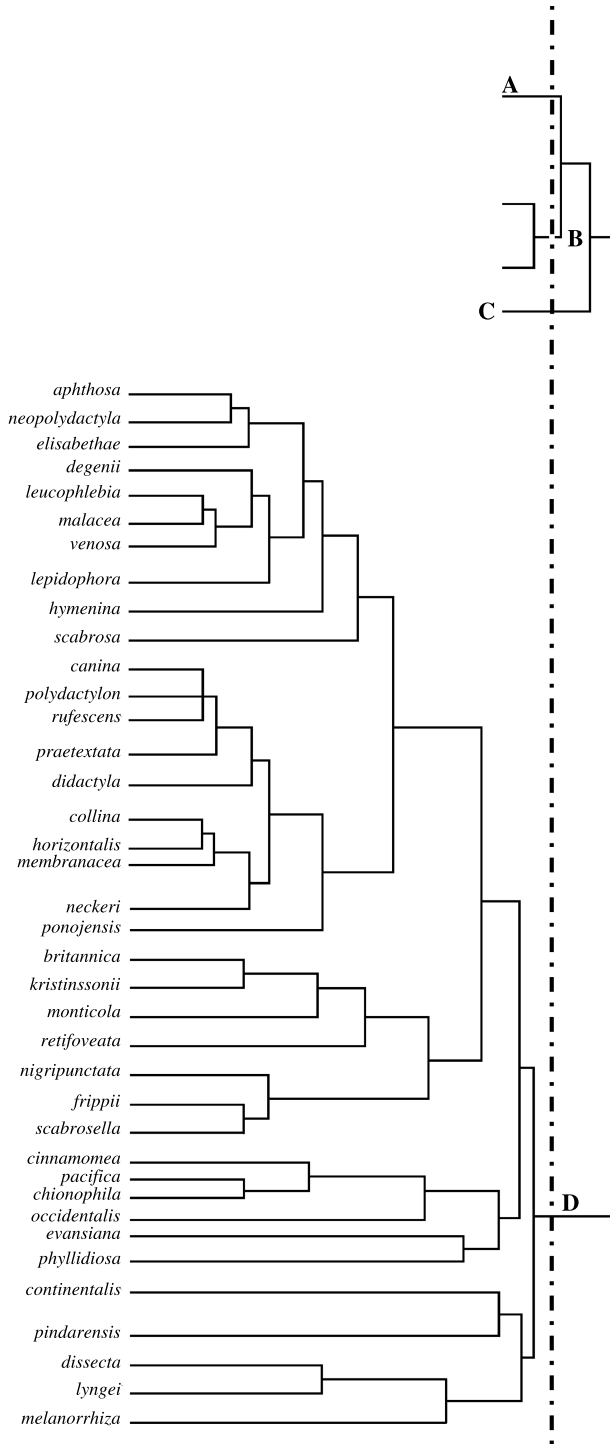


FIG. 2—continued

Europe are equivalent to western North America, both are oceanic areas and were not glaciated in the Quaternary (Brown & Lomolino 1998). *Peltigera scabrosella* is an incompletely circumpolar, boreal to arctic species restricted to north-western North America, south-western Greenland and Europe (mainly in the west of the Scandinavian Peninsula). *Peltigera frippii*, *P. retifoveata* and *P. kristinssonii* are circumpolar, boreal to arctic species, growing on the three main landmasses of the Holarctic Kingdom. Finally, *P. monticola* probably belongs to the ancient Madrean-Tethyan territory, spreading today along the calcareous mountains of Europe, North America and Asia.

The *fifth subgroup* includes five Holarctic species distributed in North America and occasionally also in other continents. This subgroup is probably made up of three phytogeographical elements: North American, North American-eastern Asian and tentatively North American-European elements (Qian 1999). *Peltigera chionophila*, *P. cinnamomea*, *P. pacifica* and *P. phyllidiosa* are North American endemics. *Peltigera cinnamomea* is endemic to central and western North America, being most abundant in the Rocky Mountains. *Peltigera pacifica* and *P. chionophila* are north-western American endemics, while *P. phyllidiosa* is an eastern American endemic. *Peltigera occidentalis* is a tentatively circumpolar, boreal to arctic species and it is known from northern North America and from Europe in the Oroscandinavian province and probably ranges from north-western Europe over the whole Siberian Taiga. On the other hand, *P. evansiana* shows an amphi-beringian pattern, growing in central Asia (Mongolia and North of China), and between 40–60°N extending from south-east to north-west of North America.

The *sixth subgroup* is made up of three endemic Asiatic species: *P. continentalis* is endemic to central Asia; *P. pindarensis* is endemic to the Western Himalayas; and *P. nigripunctata* grows only in China, Korea, Japan and the Himalayas. Furthermore, some of these endemic species spread out

through China and Mongolia to Korea and Japan, such as *P. continentalis* and *P. nigripunctata*.

Finally, the *seventh subgroup* includes three very rare and outlier species from the Holarctic. *Peltigera dissecta* is known from the Azorean Province, and *P. melanorrhiza* from the Azores as well as from western Iberian Peninsula. *Peltigera lyngei* is an arctic species known from northern Europe (Iceland and Svalbard Islands).

Provinces with the highest number of species

The biogeographic provinces with the highest number of *Peltigera* species are located in north-western North America, and the number of species decreases towards the south (Fig. 1). This pattern is very similar to that obtained by Goward & Ahti (1997), who in their study on the *Cladoniaceae* in temperate and boreal western North America observed that in North America the number of species decreases towards the south. This trend is not surprising because of the geographical orientation of the principal mountain ranges, which allowed the return to north-western North America of many species after the glacial pulses (Brown & Lomolino 1998). On the other hand, the absence of such a latitudinal trend in Europe may be related to the west-east orientation of main mountain ranges.

In Europe, the richest biogeographic provinces are located in the north, with a decreasing richness towards the south, although there is a high number of species (20 or more) in some mountainous regions of the southern half (Alps, Pyrenees, Carpathians, Cantabric mountains, etc.) (Fig. 1). In Asia, the biogeographic provinces with the highest number of species are located in the centre and east of the continent. The lowest number of species in the northern regions of Asia probably reflects the existence of many unexplored areas. The mountain habitats of South America (Andes range) and Africa (eastern mountains) harbour the highest number of

Peltigera species in their respective continents, and in Australia it is the south-east of the continent where the largest number of species are found (Fig. 1).

Finally, there are many areas in the world without any *Peltigera* records. In some cases this is to be expected, for example in the deserts of Africa, North America and Chile (Fig. 1) but, in other cases, it may be a consequence of the absence of floristic studies (e.g. many areas of Brazil). It is also worth noting that some 25% of the species treated here have been recognized and described during the last 20–25 years, and also from fairly well-known areas such as Europe. Further studies in other areas may well reveal range extensions for many species, as well as new undescribed taxa.

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Appendix 1. List of biogeographic provinces of the world

HOLARCTIC KINGDOM

BOREAL SUBKINGDOM

Circumboreal Region

Arctic Subregion

1. Oroescandinavian Province
2. Islando-Groenlandic Province
3. Asian Arctic Province
4. North American Arctic Province

Boreo-Continental Subregion

5. North European Province
6. Central Russian Province
7. Sarmatian Province
8. Western Siberian Province
9. Altai-Sayan Province
10. Middle Siberian Province
11. Transbaikalian Province
12. North-eastern Siberian Province
13. Okhotsk-Kamchatka Province
14. Canadian Boreal Province
15. Yukonian Alaska Province

Atlantic-Central European Subregion

16. Western Alpine Province
17. Eastern-Central Alpine Province
18. Apennine-Padane Province
19. Pyrenean Province
20. Central European Province
21. Subatlantic Province
22. North Atlantic Province
23. British Province
24. Cantabrian-Atlantic Province
25. Orocantabrian Province
26. Azorean Province
27. Carpathian Province
28. Tatra Province
29. Panonian Province
30. Pontic Province
31. Caucasian Province
32. Euxine Province
33. Bosnio-Illyrian Province
34. Serbo-Macedonian Province

Eastern Asiatic Region

35. Manchurian Province
36. Sakhalin-Hokkaido Province
37. Japanese-Korean Province
38. Volcano-Bonin Province
39. Ryukyu or Tokara-Okinawa Province
40. Taiwanese Province
41. Northern Chinese Province
42. Central Chinese Province
43. South-eastern Chinese Province
44. Sikang-Yünnan Province
45. Northern Burmese Province
46. Eastern Himalayan Province
47. Khasi-Manipur Province

North American Atlantic Region

48. Appalachian Province
49. Great Lakes and Central Lowlands Province
50. Prairies Province
51. Coastal Plains Province
52. Texas Prairies Province

Rocky Mountain Region

North-Western Pacific Subregion

53. Boreal Oceanic Alaskan Province
54. Cascade Province

Rocky Mountain Subregion

55. Northern Rocky Mountain Province
56. Central Eastern Rocky Mountain Province

TETHYAN SUBKINGDOM**Mediterranean Region***Western Mediterranean Subregion*

57. Aragonese Province
58. Valencian-Catalan-Provençal Province
59. Balearic Province
60. Castilian-Maestracensean-Manche Province
61. Murcian-Almeriensean Province
62. Carpetan-Iberian-Leonese Province
63. Lusitan-Extremadurean Province
64. Gaditan-Onubensean-Algarvian Province
65. Betic Province
66. Corse-Sardean Province
67. Sicula Province
68. Ligurio-Romano-Calábrica Province
69. South-western Mediterranean Province
70. Southern Moroccan Province

Eastern Mediterranean Subregion

71. Púglica Province
72. Etólico-Epirota Province
73. Peloponnesian Province
74. Crete Province
75. Tracio-Tesálica Province
76. Aegean Province
77. Cirénico-North African Superprovince
78. Steppe Eastern African Superprovince

Canarian Subregion

79. Eastern Canarian Province
80. Western Canarian Province
81. Madeirense Province

Saharo-Arabian Region (Saharo-Sindian)

82. Saharian Subregion
83. Arabian Subregion

Irano-Turanian Region*Western Asiatic Subregion*

84. Central Anatolian Province
85. Armeno-Iranian Province
86. Mesopotamian Province
87. Turanian or Aralo-Caspian Province
88. Hyrcanian Province
89. Turkestanian Province
90. Northern Baluchistanian Province
91. Western Himalayan Province

Central Asiatic Subregion

92. Central Tien Shan Province
93. Dzungano-Tien Shan Province

94. Mongolian Province
95. Tibetan Province

MADREAN SUBKINGDOM**Californian Region**

96. Northern Californian Province
97. Southern Californian Province

Great Basin Region

98. Columbian Plateau Province
99. Intermountain Province
100. Colorado Plateau Province
101. Mohave Province
102. Neomexican-Arizonian Midlands Province

Mexican Xerophytic Region

103. Baja Californian Province
104. Sonoran Province
105. Sinaloan Province
106. Chihuahuan Province
107. Tamaulipan Province

Madrean Region

108. Western Madrean Province
109. Neovolcanic-Eastern Madrean Province

PALEOTROPICAL KINGDOM**AFRICAN SUBKINGDOM****Guinean-Congolian Region**

110. Upper Guinea Province
111. Nigerian-Cameroonian Province
112. Congolian Province

Uzambara-Zululand Region

113. Zanzibar-Inhambane Province
114. Tongoland-Pondoland Province

Sudano-Zambeziian Region*Zambeziian Subregion*

115. Zambeziian Province

Sahelo-Sudanian Subregion

116. Sahelian Province
117. Sudanian Province

Eritreo-Arabian Subregion

118. Somalo-Ethiopian Province
119. South Arabian Province
120. Socotran Province

Omano-Sindian Subregion

- 121. Oman Province
- 122. South Iranian Province
- 123. Sindian Province

Karoo-Namib Region

- 124. Namib Province
- 125. Namaland Province
- 126. Western Cape Province
- 127. Karoo Province

St. Helena and Ascension Region

- 128. Ascension Islands Province
- 129. Province of St. Helena

MADAGASCAN SUBKINGDOM**Madagascan Region**

- 130. Eastern Madagascan Province
- 131. Western Madagascan Province
- 132. Southern and Southwestern Madagascan Province
- 133. Comoro Province
- 134. Mascarene Province
- 135. Seychelles Province

INDOMALESIAN SUBKINGDOM**Indian Region**

- 136. Sri Lanka Province
- 137. Malabar Province
- 138. Deccan Province
- 139. Upper Gangetic Plain Province
- 140. Bengal Province

Indo-Chinese Region

- 141. South Burmese Province
- 142. Andamanese Province
- 143. South Chinese Province
- 144. Thaiandian Province
- 145. North Indochinese Province
- 146. Annamese Province
- 147. South Indochinese Province

Malesian Region*Malesian Subregion*

- 148. Malay Province
- 149. Kalimantan (Bornean) Province
- 150. Philippinean Province
- 151. Sumatran Province
- 152. South Malesian Province

Papuan Subregion

- 153. Celebesian (Sulawesian) Province
- 154. Moluccan Province

- 155. Papuan Province
- 156. Bismarckian Province

Fijian Region

- 157. New Hebridean Province
- 158. Fijian Province

POLYNESIAN SUBKINGDOM**Polynesian Region**

- 159. Micronesian Province
- 160. Polynesian Province

Hawaiian Region

- 161. Hawaiian Province

NEOCALEDONIAN SUBKINGDOM**Neocaledonian Region**

- 162. Neocaledonian Province

NEOTROPICAL KINGDOM**CARIBBEAN-AMAZONIAN SUPERREGION****Caribbean-Mesoamerican Region**

- 163. Floridan Province
- 164. Balsas River and Southern Madrean Province
- 165. Cuba Province
- 166. Antilles Province
- 167. Veracruz-Yucatanian Province
- 168. Chiapas-Honduras Province
- 169. Panama and Costa Rica Province
- 170. Guajiran Province

Colombian-Venezuelan Region

- 171. Ecuatorian-Colombian Coastal Province
- 172. Magdalena River Province
- 173. Galapagos Islands Province
- 174. Venezuelan Highland Province
- 175. Llanos Province
- 176. Tepuis Province

Amazonian Region

- 177. Loreto Province
- 178. Negro River and High Orinoco Province
- 179. Roraima and Lower Amazonas Province
- 180. Guiana Province
- 181. Amazonas Delta Province
- 182. Acre and Madre de Dios Province
- 183. Madeira and Tapajoz Province

CHACO-BRAZILIAN SUPERREGION**Brazilian-Paranean Region**

- 184. Cerrado Province
- 185. Tocantins Province

- 186. Beni Province
- 187. Pantanal Province
- 188. Atlantic Brazilian Province
- 189. Paranean Province
- 190. Caatinga Province

Chaco Region

- 191. Boreal Chaco Province
- 192. Austral Chaco Province
- 193. Andean Chaco Province

ANDEAN SUPERREGION

Andean Region

- 194. Paramo Province
- 195. Peruvian and Bolivian Yunga Province
- 196. Peruvian Puna Province
- 197. Bolivian Interandean Province
- 198. Andean Altiplano Province

Desertic Pacific Region

- 199. Peruvian Desert Province
- 200. Atacama Desert Province

CAPE KINGDOM

Cape Region

- 201. Cape Province

AUSTRALIAN KINGDOM

North-east Australian Region

- 202. North Australian Province
- 203. Queensland Province
- 204. South-east Australian Province
- 205. Tasmanian Province

South-west Australian Region

- 206. South-west Australian Province

Central Australian or Eremaean Region

- 207. Eremaean Province

HOLANTARCTIC KINGDOM

Pampean Region

- 208. Rainy Pampean Province
- 209. Xeric Pampean Province

Middle Chile-Patagonian Region

- 210. Middle Chile Desert Province
- 211. Central Chile Province
- 212. Mediterranean Andean Province
- 213. Monte Province
- 214. Boreal Patagonia Province
- 215. Austral Patagonia Province

Valdivian-Magellanic Region

- 216. Valdivian Province
- 217. Austral Andean-Magellanic Province
- 218. Tierra del Fuego Province
- 219. Juan Fernández Islands Province
- 220. Antarctic Province

Region of the South Subantarctic Islands

- 221. Tristan-Goughian Province
- 222. Kerguelenian Province

Neozeylandic Region

- 223. Lord Howean Province
- 224. Norfolkian Province
- 225. Kermedecian Province
- 226. Northern Neozeylandic Province
- 227. Central Neozeylandic Province
- 228. Southern Neozeylandic Province
- 229. Chathamian Province
- 230. New Zealand Subantarctic Islands Province

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