



## Biogeographical analysis of two *Polypodium* species complexes (Polypodiaceae) in Mexico and Central America

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Received 14 December 2011; revised 6 March 2012; accepted for publication 6 March 2012

We analyzed the geographical and elevational distributions of two *Polypodium* complexes from Mexico and Central America. Distribution data of nine species of the *Polypodium colpodes* complex and the *Polypodium plesiosorum* complex were obtained from almost 1500 herbarium specimens, field collections in Mexico and Costa Rica, and literature studies. The presence of each species was recorded for each Mesoamerican country, in 1° × 1° grid-cells and biogeographical provinces. The rarity of species was also evaluated. Although the two complexes show extensive overlap, the *P. colpodes* complex is distributed mainly along the Pacific versant of Mexico and Central America, whereas the *P. plesiosorum* complex occurs mainly along the Atlantic versant. Those biogeographical provinces with maximum species diversity are Chiapas (seven species), Sierra Madre del Sur (six species), and the Trans-Mexican Volcanic belt (six species). Grid-cells with more species are located mainly in the mountains of central-southern Mexico and northern Central America. Richness does not decrease or increase with latitude. Elevation distributions showed that most *Polypodium* species are concentrated in the montane interval and three species groups were recognized based on elevational preferences. *Polypodium colpodes* and *P. plesiosorum* are the most widely distributed species, whereas *Polypodium castaneum* and *Polypodium flagellare* are the only two species that possess the three attributes of rarity (narrow geographical distribution, high habitat specificity, and scarce local populations). *Polypodium* species of both complexes are present mainly in the montane regions of the study area and show some degree of geographical sympatry, especially in southern Mexico and northern Central America. This overlapping is explained by the elevation tolerance within montane systems and because most species inhabit three or more vegetation types. The distributional patterns of these complexes coincided with the three regional highlands of Mesoamerica, which are separated from each other by the Isthmus of Tehuantepec and by the lowlands of Nicaragua. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, 106, 940–955.

ADDITIONAL KEYWORDS: biogeography – distributional patterns – ferns – Mesoamerica.

### INTRODUCTION

The genus *Polypodium* L. (Polypodiaceae) has a worldwide distribution, although it is more diverse in

the New World tropics, with few species in the temperate regions of America, Europe, Asia, and Africa. In a broad sense, it comprises 100–125 species (Hauffer *et al.*, 1993; Mickel & Smith, 2004). Some species traditionally included in *Polypodium* are now classified under other genera; for example, *Pleopeltis*

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and *Pecluma* (Haufler *et al.*, 1993). Recent studies of morphology and molecular data (Schneider *et al.*, 2004b; Tejero-Díez, 2005; Otto, Janssen & Kreier, 2009) have led to new generic concepts in Polypodiaceae. The *Polypodium dulce* group now appears to be polyphyletic, and most South American species formerly treated in the group (including *P. dulce*) are regarded as belonging to the genus *Pecluma*, others belong to the *Polypodium plesiosorum* group (Otto *et al.*, 2009). Species such as *Polypodium polypodioides* (Moran, 1995) are now treated as part of the genus *Pleopeltis* (Smith and Tejero, in prep.). Other groups formerly treated under *Polypodium* have been reclassified as *Serpocaulon* (Smith *et al.*, 2006) and *Phlebodium* (Tejero-Díez, Mickel & Smith, 2009).

After the above genera have been removed, the genus *Polypodium s.s.* (Otto *et al.*, 2009) comprises 42–47 species. In the last decade, the taxonomy of *Polypodium* has been redefined using cladistic comparative studies of morphology and molecular data (Schneider *et al.*, 2004b; Smith *et al.*, 2006; Otto *et al.*, 2009). In these studies, the basal clade is a group of northern temperate species (*Polypodium vulgare* L. etc., approximately 14 spp.) that ranges south to Oaxaca, Mexico. Other groups include the *P. dulce* group (Mexico to Bolivia) and its sister group, comprising the *Polypodium colpodes* complex (Mexico to Panama) plus the *Polypodium plesiosorum* complex (Mexico to Central America, northern South America, and Hispaniola). In this taxonomic sense, Tejero-Díez (2005) and Tejero-Díez *et al.* (2010) drew attention to the presence of two species complexes with homogeneous characters, which Moran (1995) recognized as the *P. plesiosorum* group. Within this last group, two complexes have been recognized: (1) *P. colpodes* (Tejero-Díez & Pacheco, 2004a), which is characterized by the type of rhizome scales (spreading and bicolorous, with the central portion reddish brown) and the prismatic-hexagonal form of the areoles formed by a netted venation; (2) *P. plesiosorum* (Tejero-Díez & Pacheco, 2004b; Tejero-Díez *et al.*, 2010) has rhizome scales tightly appressed and concolorous, and prismatic-pentagonal areoles. Extensive collections and taxonomic studies of the last two sister complexes have been carried out (Haufler & Ranker, 1995; Tejero-Díez & Pacheco, 2004a, b; Tejero-Díez, 2005). The molecular study of the groups conducted by Otto *et al.* (2009) only sampled three of the nine species recognized in the present study and further sequencing is needed.

In Mexico and northern Central America, *Polypodium* occurs mainly in montane forests, although a few species inhabit lowland forests and also dry sites (Knobloch & Correll, 1962; Siqueiros & González, 2006). In this region, *Polypodium* includes approximately 31 species with eight species endemic to

Mexico and five to Central America (Moran, 1995; Mickel & Smith, 2004).

Extensive collections and taxonomic studies of the *Polypodium plesiosorum* and *P. colpodes* complexes (Tejero-Díez & Pacheco, 2004a, b; Tejero-Díez, 2005) allowed us to prepare biogeographical analyses of these ferns. Detailed studies to obtain biogeographical data at regional and local scales are important to understand their evolutionary and biogeographical histories. In this study we evaluated the geographical distribution of all the species from both complexes, considering their geographical ranges and overlapped distribution. We also evaluated species richness in relation to elevation and latitude using three different area units: biogeographical provinces, 1 degree grid-cells, and countries. Finally, we evaluated the results to determine which physiographical features cause discontinuities in geographical distributions congruent geographical patterns were evaluated in relation to historical factors (orogeny and tectonics) that affected their distribution.

#### STUDY AREA

Mesoamerica extends from the northern border of Mexico to the eastern border of Panama and is one of the centres of biodiversity (Wilson & Johnson, 2010). The biogeography of Mesoamerica has received the attention of many naturalists since the mid-19th century (Morrone, 2005) and has been recognized and used to describe biogeographical patterns (Wilson & Johnson, 2010; Contreras-Medina, Luna-Vega & Martínez, 2011). This area includes temperate and tropical ecosystems occupying the highlands and some lowlands of Mexico, and from northern Guatemala to central Panama (Wilson & Johnson, 2010). Mesoamerica is widely recognized as a centre of exceptional species diversity and endemism, and has been placed among the main hotspots of biodiversity worldwide (Flores-Villela & Gerez, 1994; Myers *et al.*, 2000; Luna-Vega & Contreras-Medina, 2010). The extent of this hotspot is calculated at 1 130 019 km<sup>2</sup>, of which 226 004 km<sup>2</sup> (20%) remains in a more or less a natural state, and is considered critical for biodiversity conservation (Wilson & Johnson, 2010).

Some of the main factors influencing the rich biodiversity of Mesoamerica are its physiographical variation, the complex and varied climate, its mostly tropical geographical location (Campbell, 1999), and its complex geological history (Ortega-Gutiérrez, Sedlock & Speed, 1994; Campbell, 1999).

The fern flora of Mesoamerica strongly contributes to species diversity and the distinctiveness of the area. Central America is one of the most diverse regions for ferns, with approximately 2620 species, of which approximately 616 are endemic (Hassler &

Swale, 2001); Costa Rica, Panama, and Mexico are especially rich fern flora (Tryon, 1972; Tryon & Tryon, 1984; Mickel & Smith, 2004; Moran, 2008).

## MATERIAL AND METHODS

### TAXONOMIC FRAMEWORK

The two *Polypodium* complexes analyzed in the present study were selected because both have recently been studied taxonomically (Tejero-Díez & Pacheco 2004a, b; Tejero-Díez, 2005). Members of these complexes have also been extensively sampled in comparison to other *Polypodium* complexes represented in Mesoamerica.

The *P. colpodes* complex (*sensu* Tejero-Díez & Pacheco, 2004a) includes five species: *Polypodium arcanum* Maxon, *Polypodium castaneum* Maxon ex Tejero, *P. colpodes* Kunze, *Polypodium eatonii* Baker, and *Polypodium flagellare* H. Christ. The *P. plesiosorum* complex (*sensu* Tejero-Díez & Pacheco, 2004b; Tejero-Díez, 2005) comprises four species: *Polypodium conterminans* Liebm. (= *P. plesiosorum* var. *pleiolori* Tejero), *Polypodium hispidulum* Bartlett, *P. plesiosorum* Kunze, and *Polypodium rhodopleuron* Kunze. Species in both complexes are characterized by a row of fertile areoles on each side of the primary vein in the segments.

### DISTRIBUTION DATA

Distribution data for the nine *Polypodium* species were obtained from the revision of almost 1500 specimens deposited in the herbaria: B, BM, BR, C, CAS, CHAPA, CR, DS, ENCB, F, GH, IEB, INB, IZTA, K, MEXU, MICH, MO, MPU, NY, P, RB, U, UAMIZ, UANL, UC, US, and XAL (herbarium abbreviations *sensu* Holmgren, Holmgren & Barnett, 1990). In addition, floristic and revisionary studies were reviewed (Knobloch & Correll, 1962; Smith, 1981; Stolze, 1981; Mickel & Beitel, 1988; Mickel, 1992; Haufler *et al.*, 1993; Ameneyro, Fernández-Nava & Arreguín, 1995; Moran, 1995; Palacios-Ríos, 1995; Riba *et al.*, 1996; Lorea & Velázquez, 1998; Mickel & Smith, 2004; Tejero-Díez & Arreguín-Sánchez, 2004; Tejero-Díez & Pacheco, 2004a, b). Field trips were also carried out to different localities in 16 Mexican states and all departments of Costa Rica to collect specimens. With the data obtained from these sources (herbarium specimens, literature and field collections), we constructed a database that includes 768 records (database available upon request to the second author). In the present study, a record is considered to be a datum associated with a herbarium specimen collected or cited in the literature. All herbarium specimens with precise location data were geo-referenced, whereas specimens without collection data were

excluded from the analysis. Vouchers were deposited primarily at IZTA, K, MEXU, MO, and UAMIZ.

The number of records depends on the species; those with wide distributions have more records than those species with restricted distributions. This is reflected in the few specimens cited in the literature and the poor representation in herbaria of some species (Nicolalde-Morejón *et al.*, 2011).

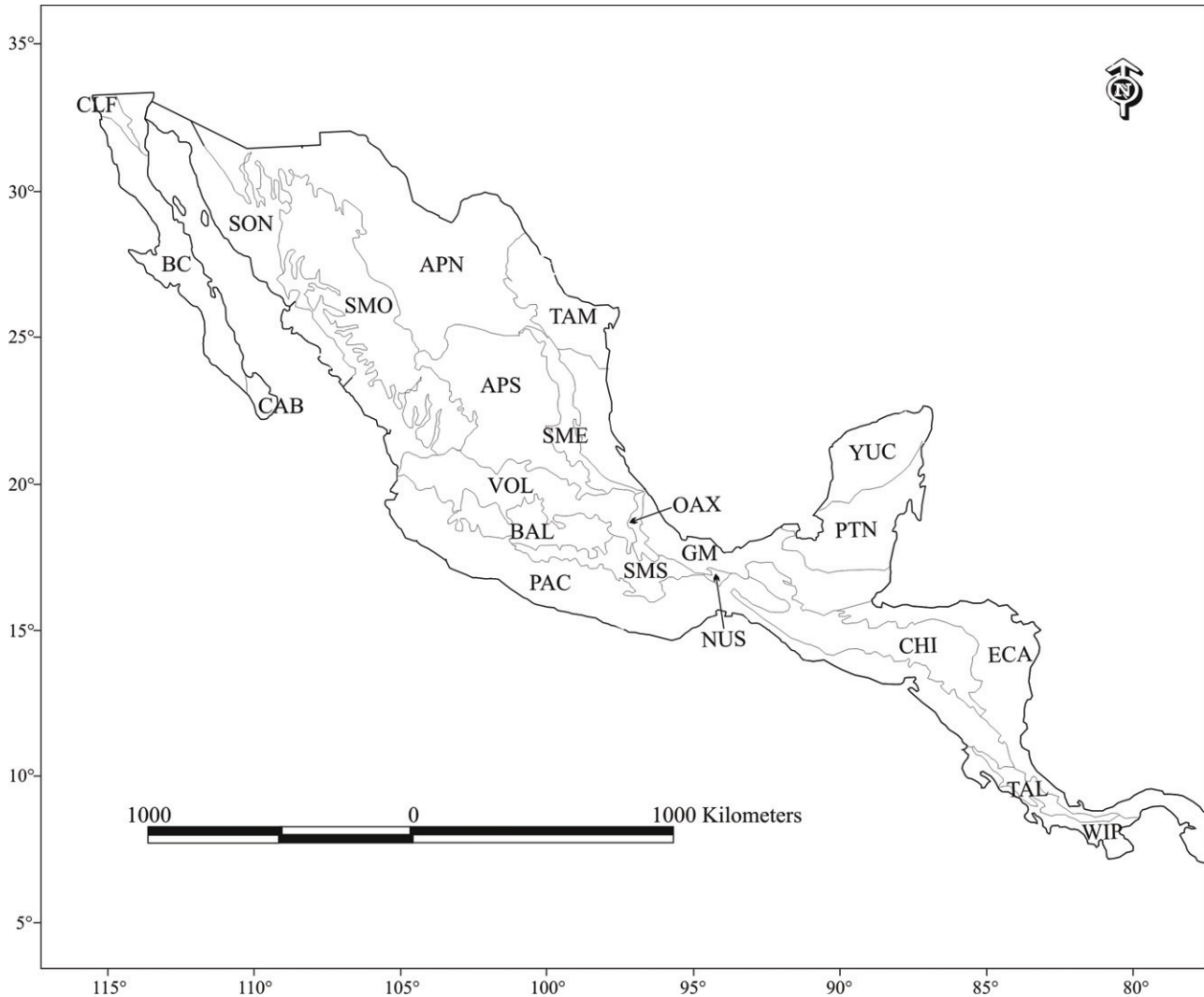
### SPECIES RICHNESS PATTERNS

Distribution maps were prepared for each of the *Polypodium* species using ARCVIEW (ESRI, 1999), a Geographical Information System. We established the distribution limits of each species in the *P. colpodes* and *P. plesiosorum* complexes using the maps of Mickel & Smith (2004) as a reference. The geographical overlap of the species ranges was also evaluated. The distribution of the nine *Polypodium* species was analyzed based on three different area units: biogeographical provinces, 1 degree grid-cells, and countries. Areas of high species richness based on these geographical units were also obtained.

Distribution maps of the nine *Polypodium* species were projected on biogeographical provinces maps using ARCVIEW (ESRI, 1999) in accordance with the regionalization proposal of Arriaga *et al.* (1997) for Mexico. For Central America, we followed the regionalization of Morrone (2006), although we also included the Talamanca province *sensu* Savage (1982) (Fig. 1). The distribution of all the *Polypodium* species were also projected on a 1 degree grid map of Mexico and Central America aiming to determine the most species richness areas for both *Polypodium* complexes. The presence or absence of each species in each grid-cell was recorded.

### ELEVATION ANALYSIS

Elevation data were obtained for all nine *Polypodium* species. The maximum and minimum limits were determined for each species, as well as the median and  $Q_1$  and  $Q_3$  (quartiles) values. These data were used to construct box plots for the species to show elevation intervals for each taxon. We also determined the preferred elevation intervals of each species using frequency histograms. These were constructed by adding records found within 300-m intervals in the elevation range 0–3000 m, thus creating ten elevation intervals. Each record was assigned to one elevation interval and all the data assigned to a particular interval were added together. Finally, elevation preferences for each species group were determined. A Kruskal–Wallis test and a multiple comparison test using STATISTICA, version 8



**Figure 1.** Biogeographical provinces of Mexico (Arriaga *et al.*, 1997) and Central America (Savage, 1982, and Morrone, 2006). Biogeographical provinces: APN, Altiplano Norte; APS, Altiplano Sur; BAL, Depresión del Balsas; BC, Baja California; CAB, Cabo; CHI, Chiapas; CLF, California; ECA, Eastern Central America; GM, Golfo de México; NUS, Soconusco; OAX, Oaxaca; PAC, Costa del Pacífico; PTN, Petén; SME, Sierra Madre Oriental; SMO, Sierra Madre Occidental; SMS, Sierra Madre del Sur; SON, Sonorense; TAL, Talamanca; TAM, Tamaulipeca; VOL, Eje Volcánico; WIP, Western Isthmus of Panamá; YUC, Yucatán.

(Statsoft Inc, 2009) was performed for the elevation data of the nine *Polypodium* species.

#### LATITUDE ANALYSIS

To evaluate the relationship between distribution patterns and latitude, we used species richness maps from the 1 degree grid-cells units. Mean species richness was calculated in belts of two degrees *sensu* Salinas-Moreno *et al.* (2004), starting at 7°N in Panama and ending at 27°N in Mexico. The species richness values included in each belt were added and

divided by the number of grid-cells with at least one species, aiming to determine the mean species richness value for each belt (e.g. in the belt of 9° to 11° there are five grid-cells with at least one species, the sum of all species values is nine, so the mean species richness value is 1.8 for that belt). The results of this analysis were displayed on a graph of mean species richness versus latitude. The belts of maximum richness were compared with selected ecological characteristics of the areas (vegetation types and elevation) and with biogeographical provinces.



## SPECIES RARITY ANALYSIS

To evaluate the rarity of each *Polypodium* species, we used the classification of Rabinowitz, Cairns & Dillon (1986), which proposed eight categories based on geographical range (wide or narrow), habitat specificity (broad or restricted), and local population size (abundant or scarce). These eight categories are formed by a combination of the aforementioned information and are: (1) wide geographical distribution, broad habitat and abundant local populations; (2) wide geographical distribution, broad habitat and scarce local populations; (3) wide geographical distribution, restricted habitat and abundant local populations; (4) wide geographical distribution, restricted habitat and scarce local populations; (5) narrow geographical distribution, broad habitat and abundant local populations; (6) narrow geographical distribution, broad habitat and scarce local populations; (7) narrow geographical distribution, restricted habitat and abundant local populations; and (8) narrow geographical distribution, restricted habitat and scarce local populations. This classification proposes that rarity should be considered along three different axes: the first axis is whether the species has a high or a low population size; the second axis is whether the species has a large or small geographical range; the third axis is whether the species can occur in a broad range of habitats or whether it is restricted to a more narrow range. According to Rabinowitz *et al.* (1986), a species could be considered common if (and only if) it has a high population size, large geographical range, and occurs in broad range of habitats; all other species are considered to be rare.

Range categories were assigned according to the number of grid-cells in which *Polypodium* species were recorded. Species recorded in less than 25% of the grid-cells of the most widely distributed species are considered to be narrowly distributed.

To assess the category of habitat specificity, we assessed the number of vegetation types with which a species has been associated. Vegetation types are based on Rzedowski (1981), who established the equivalences used by American and European botanists in relation to vegetation types present in Mexico. As a result of local population size being difficult to evaluate without demographical studies, and because these studies determine knowledge of the effective population size (Delgado *et al.*, 2008), we followed the proposal of Serrato, Ibarra-Manríquez & Oyama (2004), which only uses the total number of specimens collected in different localities in the whole study area as a reference for representing the population size. Those species with less than 25% of the maximum number of records, in relation to the *Poly-*

*podium* species with the highest number of records, were considered to have scarce local populations.

## SYMPATRIC ANALYSIS

Overlapping distributions of *Polypodium* species were analyzed with reference to the map of biogeographical provinces cited above (Fig. 1). Disjunctions were analyzed to determine whether this is the result of physiography or whether it can be attributed to the ecological nature of the habitats within each province.

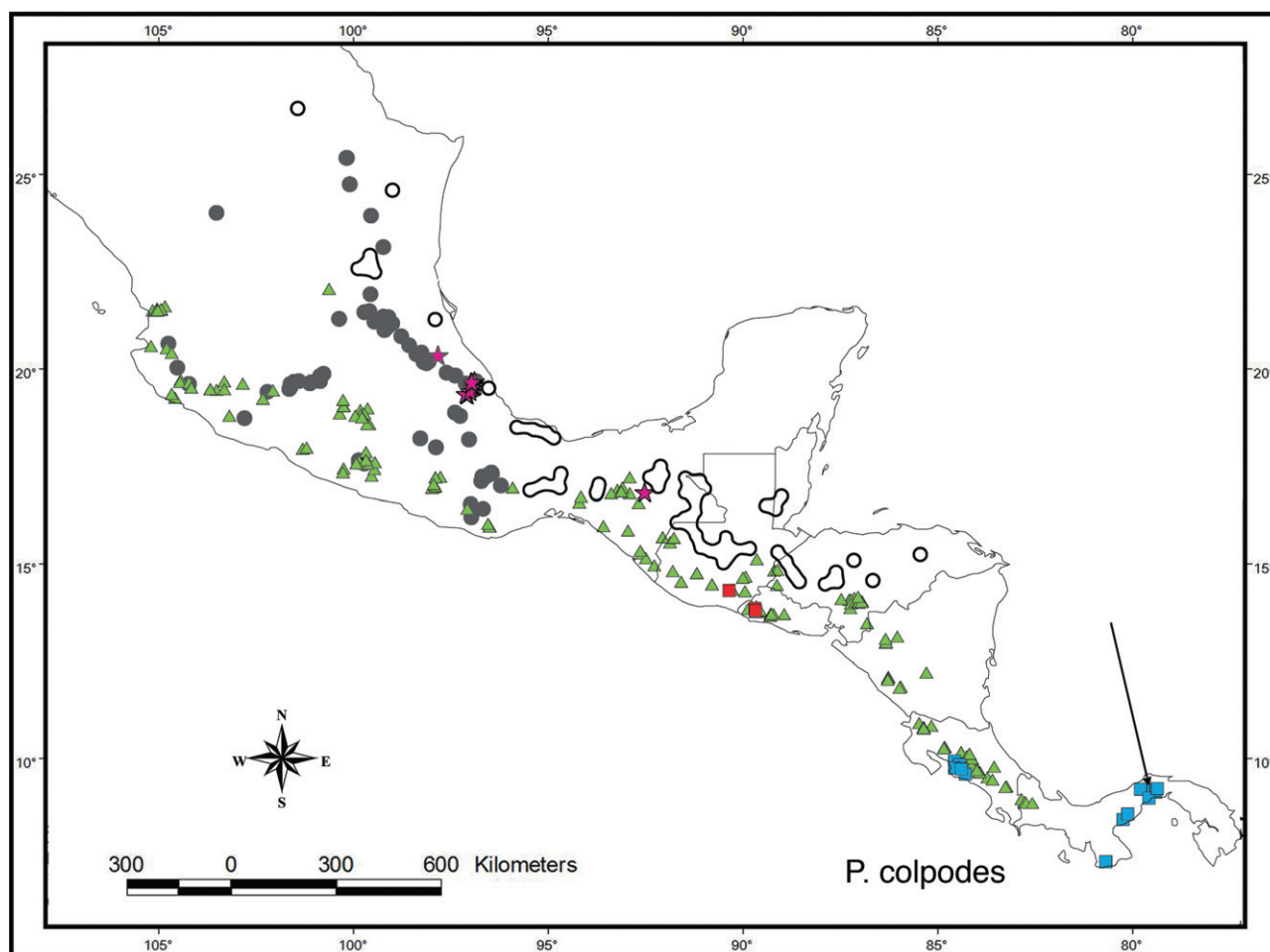
## RESULTS

## GEOGRAPHICAL RANGE PATTERNS

With the exception of *P. colpodes*, which extends into northern South America and the Greater Antilles, all the species in the *P. colpodes* and *P. plesiosorum* complexes are endemic to the study area (Figs 2, 3 and Table 1). The species of both complexes are mainly epiphytic, and, exceptionally, it is possible to find terrestrial populations, some of them epipetric (e.g. *P. plesiosorum*, *P. colpodes*, *P. conterminans* and *P. arcanum*).

Using different units of analysis (countries, biogeographical provinces, and grid-cells), we found differences in the geographical distribution patterns of the *Polypodium* species studied (Figs 2, 3, 4 and Table 1). Four species are restricted to one or two countries, whereas the remaining five are found in four or more countries. *Polypodium arcanum* and *P. eatonii* are the only species endemic to one country (Mexico). However, *P. arcanum* is widely distributed in Mexico, whereas *P. eatonii* occurs in only three Mexican states. Countries richest in these nine *Polypodium* species are Mexico ( $N = 7$ ) and Guatemala ( $N = 6$ ), followed by El Salvador, Honduras, and Nicaragua, with four species each. In Belize, *P. hispidulum* is the only known species. The biogeographical province with the most *Polypodium* species is the Chiapas (CHI), with seven species, followed by the Sierra Madre del Sur (SMS) and Eje Volcánico (VOL) provinces with six species each (Table 1; for abbreviations of the provinces, see Fig. 1).

The most widespread species are *P. plesiosorum* and *P. colpodes*, each occurring in seven countries, and *P. rhodopleuron* in four countries (Table 1). The most restricted species is *P. castaneum*, distributed in Guatemala and El Salvador, in just two grid-cells and two biogeographical provinces. The next most restricted species are *P. eatonii*, endemic to Mexico and located in four grid-cells and *P. flagellare*, in six grid-cells in Panama and Costa Rica (Table 1).



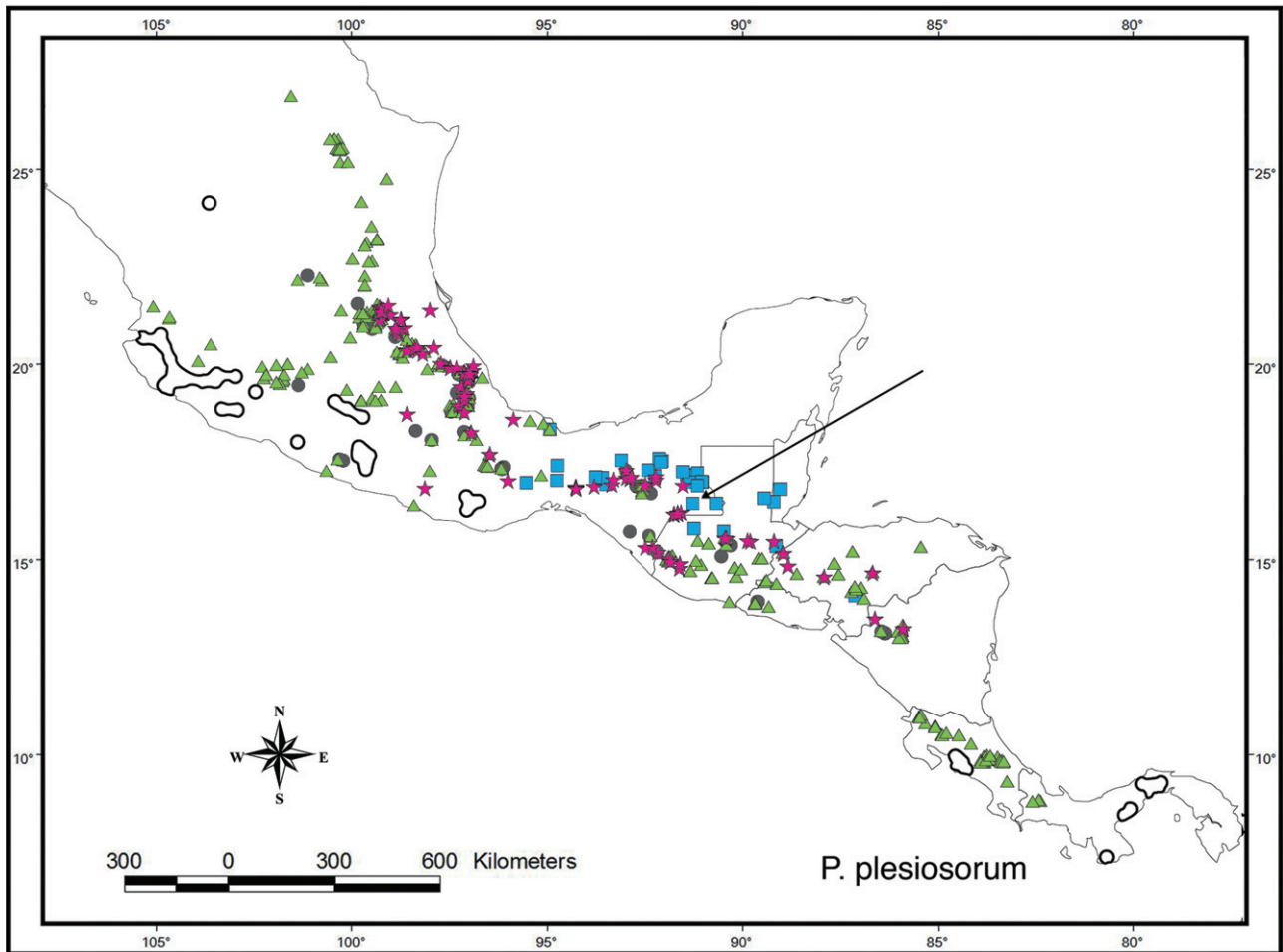
**Figure 2.** Geographical distribution of species of *Polypodium colpodes* complex: *Polypodium arcanum* (grey dots), *Polypodium castaneum* (red squares), *Polypodium flagellare* (blue squares), *Polypodium colpodes* (green triangles), and *Polypodium eatonii* (pink stars).

Only three grid-cells have a species diversity higher than 50% (five species); two are located in Sierra Madre Oriental (SME) and Eje Volcánico (VOL), and one is in Chiapas (CHI) (Fig. 4). Those grid-cells with the most species (four or five) are located in montane provinces, such as CHI, SME, SMS, and VOL, reflecting the habitat and elevational preference of these *Polypodium* species in central and southern Mexico. Rainfall in these grid-cells is an important factor influencing fern distribution (Mickel & Smith, 2004; Sanginés-Franco *et al.*, 2011). Two atmospheric phenomena have great influence in the rainfall in Mesoamerica: cold fronts, which are cold air masses that reach until 16° of latitude in the Gulf of Honduras, producing high rates of rainfall (reaching until 80% of the monthly mean); the second phenomenon is represented by depressions, hurricanes, and storms, which are produced in the Caribbean sea, generating masses of

hot and moist air, and also producing high rates of rainfall (reaching until 142% of the monthly mean) (Vargas, 2001). These two atmospheric phenomena have great impact in those grid-cells with the high number of *Polypodium* species.

#### ELEVATION DISTRIBUTION

The nine *Polypodium* species analyzed showed an overall elevation distribution extending from 100 to 3000 m a.s.l. (Table 2). The elevation range of both *Polypodium* complexes is more or less similar, with species in the *P. colpodes* complex occurring in the range 100–2650 m, whereas species in the *P. plesiosorum* occur in the range 120–3000 m. Both complexes have one species with a lowland distribution (always below the 1000 m), and a mean elevation in the range 400–500 m. The other species all have a mean elevation distribution in the range 1300–



**Figure 3.** Geographical distribution of species of *Polypodium plesiosorum* complex: *Polypodium conterminans* (grey dots), *Polypodium hispidulum* (blue squares), *Polypodium plesiosorum* (green triangles), and *Polypodium rhodopleuron* (pink stars).

2000 m (Fig. 5). The elevation ranges of the individual species are shown in Figure 5. Unfortunately, not all the records contain elevation data, and so the records used to construct the elevation interval of each species are less than those used to construct the distribution maps (Table 1). Some species, such as *P. colpodes* (156 records) and *P. plesiosorum* ( $N = 229$ ), have a wide elevational amplitude, whereas others, such as *P. castaneum* ( $N = 2$ ) and *P. eatonii* ( $N = 13$ ), have a narrower range (less than 500 m). Additional information is necessary for *P. castaneum*, which only has two elevational records. This species is rare and poorly represented in herbaria. We assume that the collection from Sta. Rosa, Guatemala (Heyde & Lux 4093, US) was made at approximately 2000 m, in similar conditions to those in the Sierra Madre de Chiapas, which extends into Guatemala, El Salvador, and Honduras. The other species and the elevational records considered were: *Polypodium arcanum*

( $N = 68$ ), *P. conterminans* ( $N = 46$ ), *P. flagellare* ( $N = 7$ ), *P. hispidulum* ( $N = 25$ ), and *P. rhodopleuron* ( $N = 73$ ).

Three species groups can be recognized based on elevation preferences: (1) a lowland group composed of *P. flagellare* and *P. hispidulum*, distributed mainly at 500 m; the first one included in the *colpodes* group (at 100 m in Madem Dam, Province of Colón, Panama) and *P. hispidulum* included in the *plesiosorum* group (at 120 m in Municipality of Ocosingo, Chiapas, Mexico) (Figs 2, 3, arrows); (2) a second group of five species (*P. castaneum*, *P. colpodes*, *P. eatonii*, *P. plesiosorum*, and *P. rhodopleuron*), distributed at 1200–1800 m; and (3) a montane group comprising *P. arcanum* and *P. conterminans*, at 1500–2400 m (Fig. 5 and Table 2). Using the categories proposed by Moran (2008), seven species occur in a middle elevation category (800–2000 m) and two in a lowland category (1–800 m).

**Table 1.** Species of *Polypodium* analyzed: the geographical distribution in Central America and Mexico (number of grid-cells and records) and occurrence in biogeographical provinces is provided for each species

Species	Distribution in Central America and Mexico	Number of grid-cells/ records	Biogeographical provinces
<i>Polypodium arcanum</i> Maxon	Mx	22/85	APS, BAL, TAM, SME, VOL, OAX, SMS
<i>Polypodium castaneum</i> Maxon ex Tejero	Gt, Sl	2/3	CHI, PAC
<i>Polypodium colpodes</i> Kunze	CR, Gt, Hn, Mx, Nc, Pn, Sl	48/185	APS, BAL, CHI, NUS, PAC, SMS, TAL, VOL
<i>Polypodium conterminans</i> Liebm.	Gt, Mx, Nc, Sl	19/53	APS, BAL, CHI, NUS, OAX, PAC, SME, SMS, VOL
<i>Polypodium eatonii</i> Baker	Mx	4/19	CHI, GM, SME, VOL
<i>Polypodium flagellare</i> H. Christ	CR, Pn	6/15	ECA, TAL, WIP
<i>Polypodium hispidulum</i> Bartlett	Be, Gt, Hn, Mx	17/29	CHI, GM, SMS
<i>Polypodium plesiosorum</i> Kunze	CR, Gt, Hn, Mx, Nc, Pn, Sl	56/286	APN, APS, CHI, ECA, GM, NUS, OAX, PAC, SME, SMS, TAM, TAL, VOL
<i>Polypodium rhodopleuron</i> Kunze	Gt, Hn, Mx, Nc	29/93	BAL, CHI, ECA, GM, SME, SMS, NUS, OAX, PAC, VOL

Geographical distribution: Be, Belize; CR, Costa Rica; Gt, Guatemala; Hn, Honduras; Mx, Mexico; Nc, Nicaragua; Pn, Panama; Sl, El Salvador. Biogeographical provinces: APN, Altiplano Norte; APS, Altiplano Sur; BAL, Depresión del Balsas; CHI, Chiapas; ECA, Eastern Central America; GM, Golfo de México; NUS, Soconusco; OAX, Oaxaca; PAC, Costa del Pacífico; SME, Sierra Madre Oriental; SMS, Sierra Madre del Sur; TAL, Talamanca; TAM, Tamaulipeca; VOL, Eje Volcánico; WIP, Western Istmo de Panamá.

**Table 2.** Species of *Polypodium* analyzed: the vegetation types sensu Rzedowski (1981) and elevation and preferential ranges (m asl) are provided for each species

Species	Vegetation types	Elevation range (m a.s.l.)	Preferential elevation interval	Mean elevation
<i>Polypodium arcanum</i> Maxon	BMM, BQ, BPQ	1145–2650	1500–2400	1959
<i>Polypodium castaneum</i> Maxon ex Tejero	BQ, BMM	1700–1800	1700–1800	1750
<i>Polypodium colpodes</i> Kunze	BG, BQ, BPQ, BTC, BTP, BTS	240–2100	900–1500	1290
<i>Polypodium conterminans</i> Liebm	BMM, BQ, BPQ	900–3000	1500–2400	1981
<i>Polypodium eatonii</i> Baker	BMM, BPQ, BG, BTC	1200–1560	1200–1500	1353
<i>Polypodium flagellare</i> H. Christ	BG, BTP, BTS	100–870	300–600	503
<i>Polypodium hispidulum</i> Bartlett	BG, BTP, BTS	120–900	300–600	403
<i>Polypodium plesiosorum</i> Kunze	BMM, BQ, BPQ, BTC, BTP	500–2900	900–2400	1591
<i>Polypodium rhodopleuron</i> Kunze	BMM, BG	700–2430	1200–1800	1474

Vegetation types: BMM, cloud forest; BC, coniferous forest; BQ, oak forest; BG, Gallery or riparian forest; BPQ, pine-oak forest; BTC, tropical deciduous forest; BTP, tropical evergreen forest; BTS, tropical semi-evergreen forest.

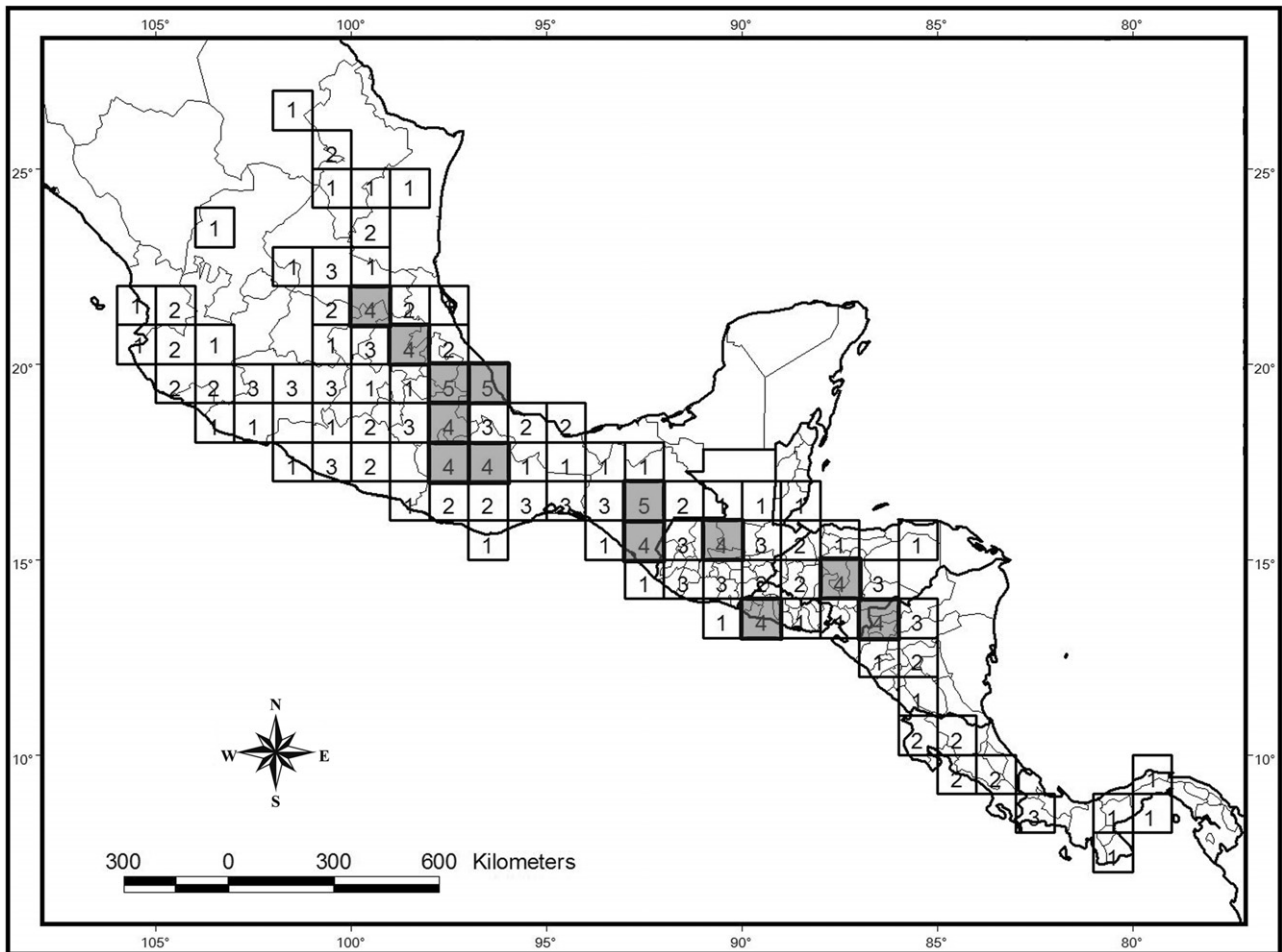
Differences in elevation among *Polypodium* species were significant ( $H = 183.7948$ ,  $P < 0.001$ ). The multiple comparison test (Table 3) showed consistency in some of the groups proposed above; for example, the pair *P. flagellare*–*P. hispidulum* and *P. arcanum*–*P. conterminans* did not have significant differences between them. By contrast, the pair *P. castaneum*–*P. eatonii* is significantly different from *P. colpodes*, *P. plesiosorum*, and *P. rhodopleuron* but, because the

first pair does not have sufficient records, we cannot suggest the existence of a fourth group.

#### LATITUDINAL DISTRIBUTION

Mean species diversity did not decrease or increase with latitude (Fig. 6). We therefore conclude that the *Polypodium* complexes analyzed in the present study did not follow a latitudinal pattern. The analysis of





**Figure 4.** Species richness of the *Polypodium colpodes* and *Polypodium plesiosorum* complexes in Mexico and Central America. Each grid-cell shows number of species present inside each grid-cell.

species richness in each grid-cell showed a low richness at the extreme ends of the study area (i.e. north-eastern Mexico and central Panama), increasing towards the 19–21° belt (southern SME and VOL) with a mean species diversity value of 2.43. The 13–15° belt (highlands of Central America present in CHI) has a mean species diversity value of 2.46. These two belts had the highest mean species diversity values in the study area.

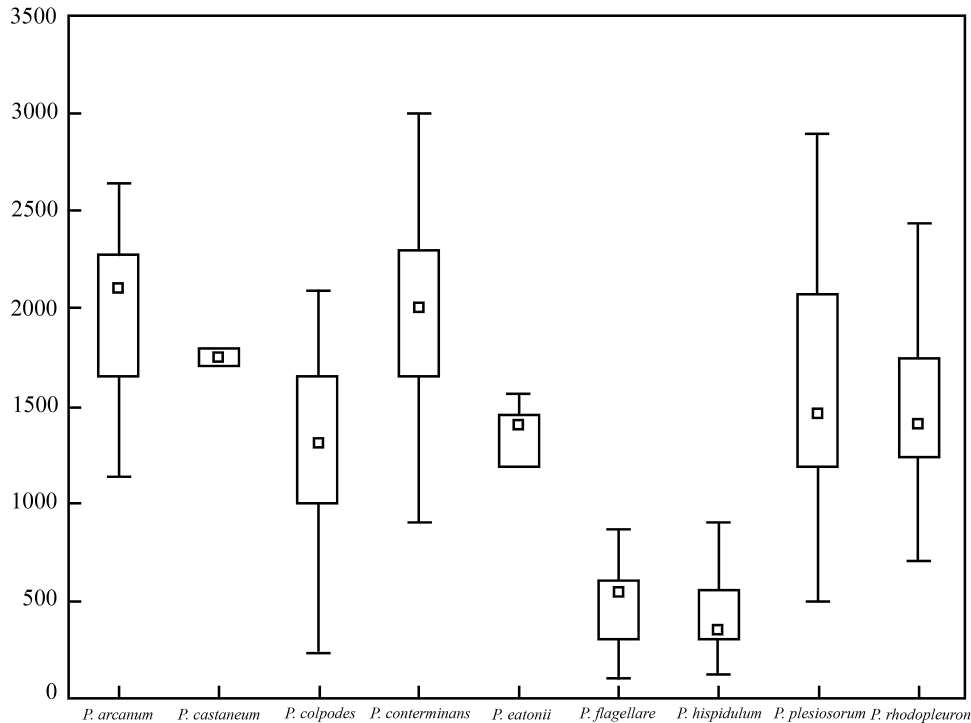
#### DISTRIBUTION AREA SIZE, HABITAT, AND RARITY

Geographical range categories were assigned based on the number of grid-cells occupied. *Polypodium plesiosorum* occurred in 56 grid-cells, the highest total. Species located in fewer than 14 grid-cells, equivalent to 25% of the maximum number, were considered to have a narrow range. Three species fall within this category (Table 1). Considering local population size, the maximum number of records (286

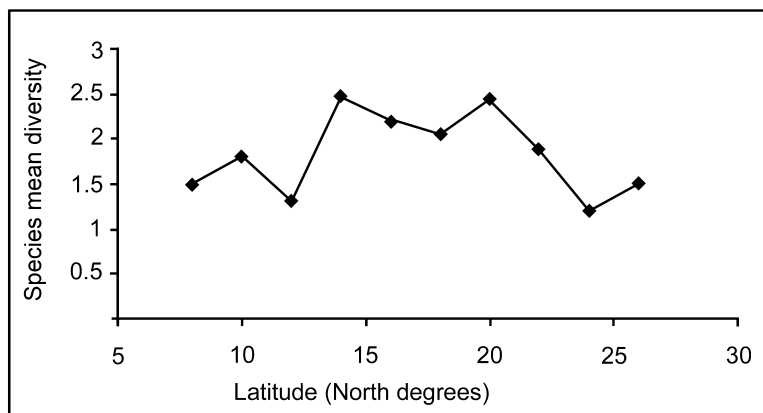
records) is also represented by *P. plesiosorum*. Five species had fewer than 71 records, which is equivalent to 25% of the maximum number. These species are considered to have small local populations (Table 1).

To determine habitat specificity, we considered the number of vegetation types *sensu* Rzedowski (1981), using *P. colpodes* as a reference, which occurs in seven vegetation types and represents the species with widest habitat specificity. Five species with restricted habitat preferences, inhabiting only two or three vegetation types were identified (Table 2).

*Polypodium colpodes* and *P. plesiosorum* are found in six and five vegetation types respectively, whereas four species inhabit three vegetation types. *Polypodium rhodopleuron* is almost restricted to cloud forests. In general, those species recorded in more than three vegetation types are distributed in both temperate and tropical forests, indicating that they are adapted to a broad range of habitats. The riparian



**Figure 5.** Elevation intervals above sea level of the nine species included in the *Polypodium colpodes* and *Polypodium plesiosorum* complexes. The box plot was constructed with median value,  $Q_1$  and  $Q_3$  (quartiles), and maximum and minimum elevation values.



**Figure 6.** Mean species diversity *versus* latitudinal distribution of the nine species included in the *Polypodium colpodes* and *Polypodium plesiosorum* complexes in Mexico and Central America.

forest represents a special case because it is found in both tropical and temperate climate regimes from sea level to 2800 m (Rzedowski, 1981).

Using the rarity classification of Rabinowitz *et al.* (1986), we assign *P. colpodes* and *P. plesiosorum* to the non-rare category, or abundant species (wide geographical distribution, broad habitat preference, and abundant local populations). A second category is formed by *P. arcanum* and *P. rhodopleuron*, which

have wide geographical distribution and abundant local populations but restricted habitat specificity. A third group is formed by *P. conterminans* and *P. hispidulum*, which have a wide geographical distribution but present restricted habitat specificity and have scarce local populations. A fourth category comprises only *P. eatonii*, which occupies a broad range of habitats but has a narrow geographical distribution and scarce local populations. Finally, *P. flagellare* and

**Table 3.** P-values (two-tailed) obtained from multiple comparisons performed after the Kruskal–Wallis test

	<i>Polypodium arcanum</i>	<i>Polypodium castaneum</i>	<i>Polypodium colpodes</i>	<i>Polypodium conterminans</i>	<i>Polypodium eatonii</i>	<i>Polypodium flagellare</i>	<i>Polypodium hispidulum</i>	<i>Polypodium plesiosorum</i>	<i>Polypodium rhodopleuron</i>
<i>Polypodium arcanum</i>	–	1.000000	0.000000*	1.000000	0.009141*	0.000000*	0.000000*	0.000015*	0.000011*
<i>Polypodium castaneum</i>	1.000000	–	1.000000	1.000000	1.000000	0.297611	0.112293	1.000000	1.000000
<i>Polypodium colpodes</i>	0.000000*	1.000000	–	0.000000*	1.000000	0.092125	0.000001*	0.000057*	0.664732
<i>Polypodium conterminans</i>	1.000000	1.000000	0.000000*	–	0.017195*	0.000000*	0.000000*	0.000727*	0.000212*
<i>Polypodium eatonii</i>	0.009141*	1.000000	1.000000	0.017195*	–	0.267133	0.004610*	1.000000	1.000000
<i>Polypodium flagellare</i>	0.000000*	0.297611	0.092125	0.000000*	0.267133	–	1.000000	0.000523*	0.005431*
<i>Polypodium hispidulum</i>	0.000000*	0.112293	0.000001*	0.000000*	0.004610*	1.000000	–	0.000000*	0.000000*
<i>Polypodium plesiosorum</i>	0.000015*	1.000000	0.000057*	0.000727*	1.000000	0.000523*	0.000000*	–	1.000000
<i>Polypodium rhodopleuron</i>	0.000011*	1.000000	0.664732	0.000212*	1.000000	0.005431*	0.000000*	1.000000	–

Asterisks indicate values that are statistically significantly different.

especially *P. castaneum* are considered rare species with narrow geographical distributions, restricted habitat specificity, and scarce local populations.

COMPARISON OF DISTRIBUTIONS

Extensive sympatry among *Polypodium* species in the biogeographical provinces is evident, mainly in provinces located between central Mexico and northern Central America. Biogeographical provinces where the distributions of four or five species overlap are: APS, CHI, PAC, DBAL, GM, NUS, OAX, VOL, SME, and SMS.

The distributions of the *P. colpodes* and *P. plesiosorum* complexes also show extensive overlap but there are important differences. The *P. colpodes* complex (Fig. 2) is present in areas of the Pacific coasts of Mexico (in Jalisco, Michoacán, Guerrero and Oaxaca), Nicaragua, Costa Rica and Panama, where the *P. plesiosorum* complex is absent. The *P. colpodes* complex is also the only one present in the Greater Antilles and northern South America. On the other hand, the *P. plesiosorum* complex occurs alone in areas of the Atlantic coast (Veracruz, Tabasco, northern Guatemala, Belize, and northern Honduras).

The *P. colpodes* complex is mainly on the Pacific side of America and the *P. plesiosorum* complex on the Atlantic side, and the same pattern is also apparent in the populations at anomalously low elevation. The *P. colpodes* complex has low elevation records towards the Pacific coast (in Costa Rica and Panama), whereas the *P. plesiosorum* complex has low elevation populations on the Atlantic side (in Chiapas and Tabasco).

The two complexes overlap in Veracruz, Oaxaca and Chiapas, which are considered Mexican states containing maximum biodiversity (Rzedowski, 1991; Mittermeier & Goettsch, 1992; Flores-Villela & Gerez, 1994); they also overlapped in Guatemala.

The distribution patterns of the nine species of *Polypodium* studied are associated with the highlands of Mexico and Central America. The highlands can be divided into three main regions: (1) the highlands north and west of the Isthmus of Tehuantepec; (2) the highlands between the Isthmus of Tehuantepec and the Nicaraguan lowlands; and (3) the highlands of Costa Rica and western Panama (Campbell, 1999; Savage, 2002).

*Polypodium arcanum* is distributed in the mountains north of the Isthmus of Tehuantepec, whereas *P. conterminans*, *P. eatonii*, and *P. rhodopleuron* are distributed north and the south of the Isthmus of Tehuantepec. The latter area appears to be an important barrier influencing the distribution of the species. *Polypodium castaneum* and *P. hispidulum* are represented in the areas between the Isthmus of

Tehuantepec and the Nicaraguan lowlands. *Polypodium colpodes* and *P. plesiosorum* are well represented in all the study areas. Their distribution too, is associated with the three highland regions noted above, although the Isthmus of Tehuantepec and the Nicaragua lowlands appeared to be important barriers influencing their more or less continuous distribution.

## DISCUSSION

Most of the species investigated in the present study inhabit temperate forests, especially in areas with humid subtropical to humid mild climates at mid-montane elevations in the range 800–2000 m a.s.l. A few species, notably *P. plesiosorum* and *P. colpodes*, inhabit both tropical and temperate forests along broad elevational and latitudinal ranges. Most species inhabit humid slopes with abundant atmospheric moisture and are protected from direct sunlight.

Several grid-cells with high number of *Polypodium* species are located in the Sierra Madre Oriental and the Trans-Mexican Volcanic Belt, two of the main Mexican mountain ranges. In these mountain chains, wet montane forests cover the eastern slopes facing the Gulf of Mexico and give rise to wet pine-oak and cloud forests in a cloud zone > 2200 m a.s.l. (Mickel & Smith, 2004). In these eastern slope areas, rainfall and fog are frequent and strongly influenced by trade winds (Hernández-Cerda & Carrasco-Anaya, 2004; Mickel & Smith, 2004). Two grid-cells with four species are located in northern Oaxaca, comprising an area that receives the highest rainfall in all the Mexican territory. Central Chiapas and the mountains of northern Central America are also areas with an extreme amount of rainfall; humidity is maintained almost all the months of the year and there is an absence of a defined dry season (Vargas, 2001). These climatic conditions, mainly maximum rainfall, cause an extremely rich fern flora comprising tree ferns, filmy ferns, and other fern groups that require constant high humidity (Mickel & Smith, 2004; Sanginés-Franco *et al.*, 2011), which are conditions that are present in those grid-cells containing four or five of the *Polypodium* species of both complexes.

The species in the *P. plesiosorum* complex are restricted to the Atlantic side of Mesoamerica. By contrast, species in the *P. colpodes* complex are restricted to the Pacific side of Mesoamerica and the Greater Antilles. The Caribbean plate originated in the Pacific Ocean and moved gradually eastward, passing between the North and South American plates before reaching its present position during the Miocene (Kerr *et al.*, 1999). Some groups with similar distributions in eastern (Atlantic) and western (Pacific) Mexico

are known (Flores-Villela & Goyenechea, 2001) and Contreras-Medina, Luna-Vega & Morrone (2007) found a close relationship between the eastern and western Mexican provinces using reptiles and gymnosperms, respectively. An example of this link is the sister group relationship between two species of *Dioon* (Zamiaceae): *Dioon tomasellii* is distributed in the Pacific slope and *Dioon edule* is found in the Gulf of Mexico slope (Moretti *et al.*, 1993). The *Rana pipiens* complex includes sister species distributed in western and eastern Mexico (Flores-Villela & Goyenechea, 2001). The biogeographical connection between western Mexico and the Greater Antilles has also been noted in other plant taxa, as suggested by previous studies (Standley, 1936; Rzedowski, 1981; Diego-Pérez *et al.*, 1997). Escalante *et al.* (2007) analyzed the distribution in 40 plant and animal taxa in Mexico and found that the major division is between the ‘western’ (i.e. Pacific) and ‘eastern’ (i.e. Atlantic) sectors. This fundamental division contrasts with the more common north/south division or Nearctic and Neotropical biogeographical regions.

The distribution of species in the *P. plesiosorum* and *P. colpodes* complexes is related to the formation of the land bridge between North America and South America. Other factors that may have influenced the distribution of the species are the expansion and contraction of forests in Mexico and Central America during the Cenozoic as a result of climatic change (such as the Eocene–Oligocene cooling; Zanazzi *et al.*, 2007), Pleistocene cooling and marine transgressions (Bartlett & Barghoorn, 1973; Graham, 1973; Rzedowski, 1981; Coney, 1982; Gómez, 1982; Prance, 1982; Toledo, 1982; Zanazzi *et al.*, 2007), and tectonic events (Ortega-Gutiérrez *et al.*, 1994). Uplift of the main mountain chains in the region (the Sierra Madre Occidental, Sierra Madre Oriental, Trans-Mexican Volcanic Belt, and Sierra Madre del Sur) occurred mainly during the Cenozoic in Mexico and Central America (Ortega-Gutiérrez *et al.*, 1994). Orogeny may have been the chief factor driving speciation in the area, as suggested for *Pinus* (Farjon & Styles, 1997). Orogeny in the region may also explain how the Pacific *P. colpodes* complex and the Atlantic *P. plesiosorum* complex were both ‘trapped’ in Mexico.

Pleistocene cooling, including the last glaciation caused a reduction and fragmentation of the Mesoamerican forests. This may have led to the reduction in the distribution ranges of species with warm and humid climatic requirements (such as *P. castaneum*, *P. eatonii*, and *P. flagellare*). By contrast, it is expected that species less restricted to warmer and subhumid habitats (such as *P. plesiosorum*, *P. colpodes*, and *P. arcanum*) may have increased their distribution. Others probably suffered fragmentation as a result of geographical isolation and evolved



different geographical varieties (Mickel & Smith, 2004; Tejero-Díez & Pacheco, 2004a, b).

Species in the *P. colpodetes* complex show clear elevation and rainfall preferences; *P. arcanum* and *P. castaneum* are located in temperate forests, whereas *P. colpodetes* and *P. eatonii* inhabit both tropical and temperate forests, and *P. flagellare* is restricted to tropical forests. Similarly, species of the *P. plesiosorum* complex, *P. conterminans*, and *P. rhodopleuron* are confined to temperate forests; *P. plesiosorum* inhabits both tropical and temperate forests; and *P. hispidulum* is restricted to tropical forests.

Considering the species diversity of both *Polypodium* complexes, we noted that there is no affinity between latitude and species diversity. However, two regions were noted: one in Central Mexico and another between Mexico and Guatemala. This may be ascribed to these complexes have with the speciation events that has given rise to the Mesoamerican biodiversity hotspot, as we see in amphibians, reptiles (Wilson & Johnson, 2010), and cycads (Nicolalde-Morejón *et al.*, 2011).

In the present study, we concluded that one of the main vicariance events that has led to the fragmentation of the ancestral range of the species studied occurred in the Isthmus of Tehuantepec region. The *Polypodium* complexes studied represent the Central American component of the pteridoflora, which suffered fragmentation and isolation from their northern congeners, of the *P. dulce* group. A combination of physiographical and climatic factors associated with a complex geological history fragmented and modified portions of the ancestral habitats (Campbell, 1999). The biota of Mesoamerica is a complex assemblage of biological groups with diverse histories (Campbell, 1999; Morrone, 2006; Luna-Vega & Contreras-Medina, 2010). The biota of this area has sometimes been compared with biota in North America and, in other events, it has been compared with the South American biota. However, the biota of this region has been considered to represent a distinctive unit as a result of the high level of endemism (Rzedowski, 1991; Campbell, 1999). The *Polypodium* complexes analyzed have a clear North American affinity. Because most of these species are endemic to Mesoamerica, they contribute to the recognized centre of endemism.

The geological history of Mexico and Central America resulted in the formation of the mountain ranges harbouring the *Polypodium* species. The origin of the three main highlands of Mesoamerica is the result of the interaction of the North American and Caribbean tectonic plates with the Cocos plate, resulting in the subduction of the latter. The interaction between the Cocos and the Caribbean plates resulted in the formation of the highlands that extends from

Chiapas (Mexico) to Nicaragua, whereas the interaction between the North America and Cocos plates resulted in the uplift of the highlands of central and southern Mexico (Ortega-Gutiérrez *et al.*, 1994). The movement of the Chortis block from its original position (adjacent to the Guerrero and Oaxaca states in Mexico) to its current position (mainly the recent Guatemala and Honduras territories), between 6 and 10 Mya (Savage, 2002), contributed to the establishment of the northern part of Central America (Cevallos-Ferriz & González-Torres, 2005). The formation of the land bridge is geologically speaking therefore relatively recent, taking place in the late Pliocene, as recently as 3.5 Mya (Savage, 2002; Cevallos-Ferriz & González-Torres, 2005). These recently formed landscapes were occupied by plants that were formerly part of higher latitude communities in North America (Cevallos-Ferriz & González-Torres, 2005). This implies that the *Polypodium* species or their ancestors could not have migrated from the north into Central America more than 6 or 7 Mya years ago. Subsequent speciation associated with the highlands may have occurred, producing the distributional patterns observed today in the two *Polypodium* complexes.

Most of the species in the two *Polypodium* complexes are montane ferns; the majority of the species have a mean elevation above 1200 m a.s.l. Exceptions are *P. flagellare* and *P. hispidulum*, which inhabit lowlands with tropical vegetation and their elevation intervals are located < 1000 m. None of the *Polypodium* species analyzed in the present study is restricted to any biogeographical province, supporting the observation that fern species in general are more widely distributed than flowering plant species. This may be attributed to spore dispersal, which is generally greater than that of seeds, or because there has been less allopatric evolution in ferns.

Congruence in species distributions could be the result of two scenarios. First, most of the *Polypodium* species in this study inhabit three or more vegetation types. This tolerance has permitted the co-existence of more than one species in several areas that exhibit both tropical and temperate climatic conditions. Second, a high elevation tolerance of most *Polypodium* species has permitted their coexistence at similar elevations.

*Polypodium conterminans*, *P. plesiosorum*, and *P. rhodopleuron* occur in most of the provinces in the study area. Despite the high vagility of ferns, the results of the present indicate that any pair of provinces has different assemblages of *Polypodium* species. This may be explained by the climatic characteristics that prevail in each biogeographical province and the relationship of each *Polypodium* species to environmental conditions, especially in the case of

those considered with habitat specificity. Historical factors, as yet unexplored, may also have been important.

Although ferns have a high potential vagility in relation to other vascular plants, the distributional patterns reported in the present study are congruent with those reported previously for other taxa, and so they can be incorporated into general statements about the biogeography of montane groups in Mesoamerica.

Mesoamerica is an area of exceptionally high biotic diversity (Myers *et al.*, 2000). The *Polypodium* complexes investigated in the present study form part of this biodiversity. Other Polypodiaceae genera (e.g. *Pleopeltis* and *Pecluma*) are also diverse in this region (Otto *et al.*, 2009). Montane zones generally constitute areas of particular biogeographical and evolutionary interest (Barrington, 1993; Wolf, Schneider & Ranker, 2001; Contreras-Medina *et al.*, 2007). This is also true for the *Polypodium* species in the two complexes studied. The present study furthermore indicates that fern distribution data can contribute to the knowledge of Mesoamerican biota and biogeography.

#### ACKNOWLEDGEMENTS

We thank Alan R. Smith, Blanca Pérez García, Juan J. Morrone, and an anonymous reviewer for useful comments on the manuscript. We are also indebted to the staff of the herbaria cited in the text for their courtesy during our review of specimens, especially Olga Martha Montiel and James C. Solomon at MO. Assistance in the field was provided by Luisa S. Sandoval Moran, in Mexico, and F. Alexander Rojas Alvarado, in Costa Rica. The figures were prepared by Andrés González, Santiago Ramírez, César Andrés Torres, and Julio Ramírez. The formation of the taxonomic database was supported by a Research Doctoral Fellowship number 160 253 from the Consejo Nacional de Ciencia y Tecnología, Mexico (CONACYT) given to the second author. Support from projects FOSEMARNAT-2004-C01-311 and DGAPA-PAPIIT IN221711 is gratefully acknowledged.

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