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## Research article

# Distribution and conservation status of *Phlegmariurus* (Lycopodiaceae) in the state of Veracruz, Mexico

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### Abstract

The fern and lycophyte flora of Mexico contains 13 species in the genus *Phlegmariurus* (Lycopodiaceae; club moss family), of which nine are found in the state of Veracruz (*P. cuernavacensis*, *P. dichotomus*, *P. linifolius*, *P. myrsinites*, *P. orizabae*, *P. pithyoides*, *P. pringlei*, *P. reflexus*, *P. taxifolius*). They are located primarily in undisturbed areas of humid montane, pine-oak and tropical humid forests, which are all ecosystems threatened by deforestation and fragmentation. The objective of this study was to evaluate and understand the distribution and conservation status of this genus in the state of Veracruz, Mexico. Using Maxent, probability distributions were modeled based on 173 herbarium specimens (25% from recent collections by the authors and/or collaborators), considering factors such as climate, elevation and vegetation cover. Additionally, anthropogenic impacts on the original habitat of each species were analyzed in order to assign threatened categories based on IUCN classifications at regional levels. Results show that potential distributions are located in the montane regions of the central and southern parts of the state. All nine *Phlegmariurus* species in Veracruz were found to be in some category of risk, with *P. orizabae* classified as critically endangered, having only a single specimen collected in 1854. The main reasons for species threats are the continuous loss and fragmentation of their natural habitat, uncontrolled harvesting activities, and the lack of protected areas that include humid montane and pine-oak forests in the central region of the state.

**Keywords:** Maxent, IUCN Red List, endangered species, ferns and lycophytes, *Huperzia*, anthropogenic disturbance.

### Resumen

La flora de helechos y licófitos de México comprende 13 especies del género *Phlegmariurus* (Lycopodiaceae), de las cuales nueve se encuentran en el estado de Veracruz (*P. cuernavacensis*, *P. dichotomus*, *P. linifolius*, *P. myrsinites*, *P. orizabae*, *P. pithyoides*, *P. pringlei*, *P. reflexus*, *P. taxifolius*). Se distribuyen principalmente en zonas conservadas del bosque mesófilo de montaña, bosque de pino-encino, así como selva alta y mediana perennifolia, que son ecosistemas amenazados por deforestación y fragmentación. Por lo anterior el objetivo planteado es conocer y evaluar la distribución y el estado de conservación de las especies de este género. Se realizó una modelación con base en 173 especímenes de herbario (el 25% corresponden a colectas recientes de los autores y/o colaboradores) con el programa Maxent, considerando factores climáticos y de elevación, así como los tipos de vegetación. Además se analizó el impacto antrópico sobre el hábitat original de las especies, con la finalidad de asignarles una categoría de riesgo, según criterios de la UICN a nivel regional. Los resultados muestran que la distribución potencial se localiza principalmente en las zonas montañosas del centro y sur del estado. Las nueve especies de *Phlegmariurus* en Veracruz se encuentran en alguna categoría de riesgo, destacando *P. orizabae* clasificada en peligro crítico, ya que se conoce sólo del ejemplar tipo realizado en 1854. Las razones principales de la amenaza a las especies son la continua pérdida y fragmentación de los hábitats naturales, el saqueo incontrolado y la falta de áreas protegidas que incluyan el bosque mesófilo y pino-encino en la región central del estado.

**Palabras clave:** Maxent, Lista Roja de la UICN, especies en riesgo, helechos y licófitos, *Huperzia*, perturbación antrópica.

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## Introduction

The Lycopodiaceae (club mosses) is a cosmopolitan family of about 430 homosporous lycophytes (including 185 Neotropical species) in which the species exhibit shoot-forms correlated with habitat [1-4]. Until recently, the most widely adopted four-genus classification of Øllgaard [5] recognized *Lycopodium* L., *Lycopodiella* Holub, *Huperzia* Bernh., and *Phylloglossum* Kunze. However, recent molecular phylogenetic investigations of the family have shown that *Huperzia* is paraphyletic [6]. Thus, *Phlegmariurus* Holub is now recognized as a genus sister of *Huperzia* [7, 8] and includes a broad spectrum of mostly epiphytic species with pendulous sporophyllous shoots lacking gemmae. *Phlegmariurus* occurs primarily in tropical and subtropical regions, whereas *Huperzia sensu stricto*, of Wagner and Beitel [9] includes only terrestrial species with erect shoots bearing gemmae in leaf axils [2].

The fern and lycophyte flora in Mexico comprises 13 species in the genus *Phlegmariurus*, of which nine species are found in the state of Veracruz [10, 11]. They are generally distributed in undisturbed zones of humid montane, pine-oak and tropical humid forests [10]. In Mexico as well as in Veracruz, these ecosystems are being reduced and degraded by deforestation and land use change for the establishment of agricultural and pasture land [12]. This impacts natural habitats and reduces species richness and populations of vascular plants in general, including fern and lycophytes and the *Phlegmariurus* species in particular. Species of this genus have been found to be absent or rare in disturbed humid montane and secondary forests, remnant trees, and coffee plantations in central Veracruz [13-16]. This rarity or absence is because of the general dependence of vascular epiphytes on mature host canopy trees, and also their vulnerability to changes in micro-climate to the drier and warmer conditions present in disturbed and secondary forests [17-19].

Moreover, some of the *Phlegmariurus* species are being harvested from their natural habitat and sold in local markets of Veracruz and other states like Oaxaca for ornamental purposes [20, 21]. In general, species of *Phlegmariurus* in Mexico are very poorly represented in regional or national herbaria, and some species are represented by only a few specimens collected decades ago, as is the case with *P. cuernavacensis* and *P. orizabae* in Veracruz [10, 22]. The lack of knowledge about

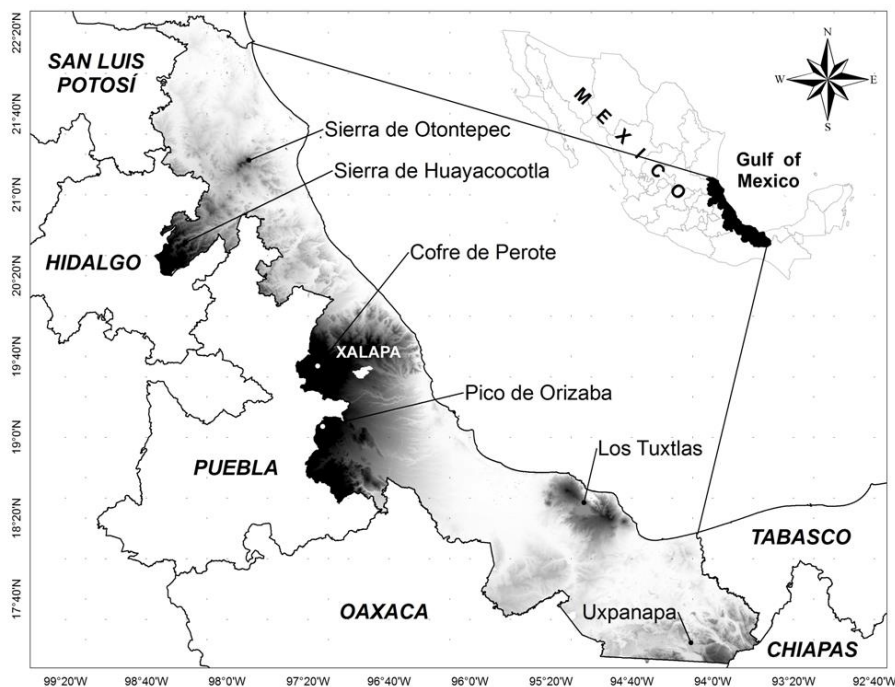
their distribution suggests that most of them are rare species of conservation concern. According to a preliminary evaluation by Tejero-Díez et al. [11], all *Phlegmariurus* species are classified under a risk category, despite the fact that in the official Mexican Red List only one species (*P. dichotomus*) is classified as threatened [23].

Our objective was to learn with more detail the distribution of *Phlegmariurus* species in order to determine their conservation status, comparing their actual and potential distribution in Veracruz. In this study we modeled the potential distribution of species in the genus for the state, using the Maxent software based on herbarium samples, as well as considering climatic factors, elevation, and vegetation cover. Furthermore, anthropogenic impact on the natural habitat of the species was evaluated in order to assign a threatened category according to their conservation status, using the IUCN criteria at regional levels [24, 25].

## Methods

### Study area

The state of Veracruz has a total area of *ca.* 72,000 km<sup>2</sup>, divided into 212 municipalities [26]. It is located in eastern Mexico along the coast of the Gulf of Mexico in a transition zone between two biogeographic regions: Nearctic and Neotropical [27]. Its geography encompasses two extensive coastal plains broken up by four important mountain ranges: i) the *Sierra Madre Oriental*, which contains the *Sierra de Huayacocotla* in the northern portion of the state; ii) the *Eje Neovolcánico*, with two of the highest peaks in Mexico, *Pico de Orizaba* (5,610 m) and *Cofre de Perote* (4,280 m); iii) the *Sierra de Los Tuxtlas* in the southern part of the state, with elevations up to 1,700 m; and iv) the *Sierra Madre del Sur*, which in its northwestern portion forms the *Sierra de Zongolica*, with elevations up to 2,500 m [28] (Fig. 1).



**Fig. 1.** Map of Veracruz and bordering states, Mexico, indicating Otontepec, Huayacocotla, Los Tuxtlas and Uxpanapa area, as well as the central montane region around the capital city of Xalapa, as relevant areas for the distribution of *Phlegmariurus* species.

The heterogeneous geomorphology of Veracruz creates a wide variety of climate types, from warm tropical-dry to cold temperate-humid climates [29]. This variety of climates and the montane terrain delimit the presence of 19 vegetation types, including humid montane, pine-oak and tropical humid forests, which are considered the most diverse ecosystems in Mexico [30]. The combination of the above factors places Veracruz among the three most biodiverse states in the country, with a vascular flora of close to 7,800 species [30], of which about 570 species are ferns and lycophytes [31, 32].



**Fig. 2. *Phlegmariurus* species of Veracruz: a) Detail of *P. myrsinites*, b) *P. pringlei* in habitat, c) *P. taxifolius* in habitat, d) Type specimen of *P. orizabae* (image courtesy of the C. V. Starr Virtual Herbarium of The New York Botanical Garden), e) *P. linifolius* sold in a gift shop, f) *P. pringlei* and *P. taxifolius* sold at a local market in Xalapa.**

### Database

The present study is based on the revision of 260 herbarium specimens (including duplicates in several herbaria) and high resolution digital photographs of all nine *Phlegmariurus* species (*P. cuernavacensis*, *P. dichotomus*, *P. linifolius*, *P. myrsinites*, *P. orizabae*, *P. pithyoides*, *P. pringlei*, *P. reflexus*, *P. taxifolius*; Fig. 2) recorded for the state of Veracruz, Mexico, which were deposited in a total of 13 herbaria (Table 1). Of a total of 173 revised collections (Appendix 1), including 25% recent collections by the authors and/or collaborators, the following data were obtained from the specimen labels: species (the correct taxonomic determination was confirmed for each revised specimen), information on the collector, collection number, determiner, municipality, locality, elevation, date, habitat, life form, latitude, longitude, size, and abundance. The collection years of the specimens range from 1828 to 2014, which were grouped into five periods (modified from Zizka et al. [33]): i) 1828 to 1920; ii) 1921 to 1965; iii) 1966 to 1985; iv) 1986 to 2000; and v) recent collections from 2001 to 2014. This was done with the goal of identifying the temporality and intensity of species collections during these periods, and based on these parameters, be able to characterize species distributions and rarity, as well as to evaluate the threats through time.

Geographic distribution at global, state, and municipality levels in Veracruz, as well as the vegetation type and the elevational range where species occur in Veracruz are listed for each species. A single voucher specimen is cited for each municipality.

Table 1. Information on consulted herbaria and the number of revised specimens of *Phlegmariurus* species collected in the state of Veracruz, Mexico (41 of these with duplicates in several herbaria).

Herbarium	Acronym	Specimens
Instituto de Investigaciones Biológicas, Universidad Veracruzana, Xalapa, Veracruz	CIB	31
Herbario de la Facultad de Ciencias Biológicas y Agropecuarias, Universidad Veracruzana, Córdoba, Veracruz	CORU	14
Estación de Biología Tropical "Los Tuxtlas", UNAM, San Andrés Tuxtla, Veracruz	EBT (unofficial)	14
Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Distrito Federal	ENCB	6
Field Museum of Natural History, Chicago	F	2
Herbario Nacional de México, Universidad Nacional Autónoma de México, Distrito Federal	MEXU	52
Missouri Botanical Garden, St. Louis	MO	8
New York Botanical Garden, New York	NY	1
Marie Selby Botanical Gardens, Sarasota	SEL	4
División de Ciencias Biológicas y de la Salud, Universidad Autónoma Metropolitana Iztapalapa, Distrito Federal	UAMIZ	40
University Herbarium, University of California, Berkeley	UC	25
Instituto de Ecología, A. C., Xalapa, Veracruz	XAL	50
Herbario de la Facultad de Biología, Campus Xalapa, Universidad Veracruzana, Xalapa, Veracruz	XALU	13
		<b>Total: 260</b>

#### *Potential distribution*

The Maxent v.3.3 model was used [34] to obtain the potential distribution of the *Phlegmariurus* species in Veracruz. This model is based on a statistical approximation called maximum entropy, which formulates predictions using incomplete information, in this case data on the presence of the species to estimate its potential distribution [34-35]. The coordinates of the localities of each collected specimen are an important factor in this study; for specimens that lacked this information it was therefore necessary to derive an approximation based on location data described on the label. Ten of the previously collected specimens were not considered in this analysis, (marked with the “?” symbol under “Representative specimens from Veracruz”), due to their locality being doubtful and the inability to assign reliable coordinates. Moreover, it was impossible to estimate potential distribution of *P. orizabae* since there was only a single known specimen.

Spatial data used for the Maxent model included land use and vegetation cover at 1:250,000 scale [36]. In addition, we used twenty climate data variables from the BioClim database of WorldClim [37]: altitude, annual mean temperature, mean of monthly maximum and minimum temperature, isothermality, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter and precipitation of coldest quarter. All spatial data layers were converted to ASCII format using the software ArcGIS Ver 9.3 of ESRI®. AUC values are used to describe model performance or predictive accuracy.

#### *Conservation status*

The classification of conservation status is based on the categories and criteria proposed in the IUCN Red List at regional levels [24, 25]: Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), and Least Concern (LC). These categories were assigned based on our extensive database, as well as land use and land cover data [32] from Semarnat [38] and Ellis et al. [12], which use Landsat imagery to evaluate land use and forest cover change within two time periods (1990 and 2000). Additionally, we consulted national level results on anthropogenic threats to different vegetation types and their implications on biodiversity loss [39]. Our evaluation is reinforced by information presented by CONABIO [40], which characterizes the issue of humid montane forest loss in Mexico.

The considerable recent collections made by the authors and/or collaborators, together with own observations in the field, support our ability to assess the conservation status of *Phlegmariurus* species in Veracruz, which also requires field experience. The information generated by Maxent was useful in reinforcing our conclusions and proposals for conservation of species.

Starting from the label information for each herbarium specimen, we calculated for each species the Area of Occupancy (AOO), defined as the area of suitable habitat currently occupied by the taxon, excluding cases of vagrancy [41]. Furthermore, considering the potential distribution modeled by Maxent, we estimated the Extent of Occurrence (EOO), defined as the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon, excluding cases of vagrancy [41]. These two measurements represent different aspects of geographical range size: AOO provides information on the area of suitable habitat, whereas EOO provides information on overall geographical spread [42, 43].

The surface area for AOO and EOO was obtained from the vegetation and land use cover layer [36] using ArcGIS 9.3. Although we assume that we have the best available database to assess conservation status of *Phlegmariurus* species from Veracruz based on geographic distribution, a detailed survey of population level is lacking for all of them. The distribution area in km<sup>2</sup> was therefore compared with IUCN criterion B (Geographical Distribution), which allows a species to qualify as threatened when its geographic range is restricted (Table 2), but does not require population size data (needed in criteria A, C and D) to assign risk status [43]. Under criterion B, a

species should also meet at least two of the following conditions: severe fragmentation or existence at few locations; continuing decline; and/or extreme fluctuations [24, 25].

Table 2. Thresholds for geographical range (Criterion B) according to IUCN [25].

	Threatened (km <sup>2</sup> )			Not threatened (km <sup>2</sup> )
	Critically Endangered	Endangered	Vulnerable	
B1. Extent of occurrence (EOO)	<100	<5,000	<20,000	>20,000
B2. Area of occupancy (AOO)	<10	<500	<2,000	>2,000

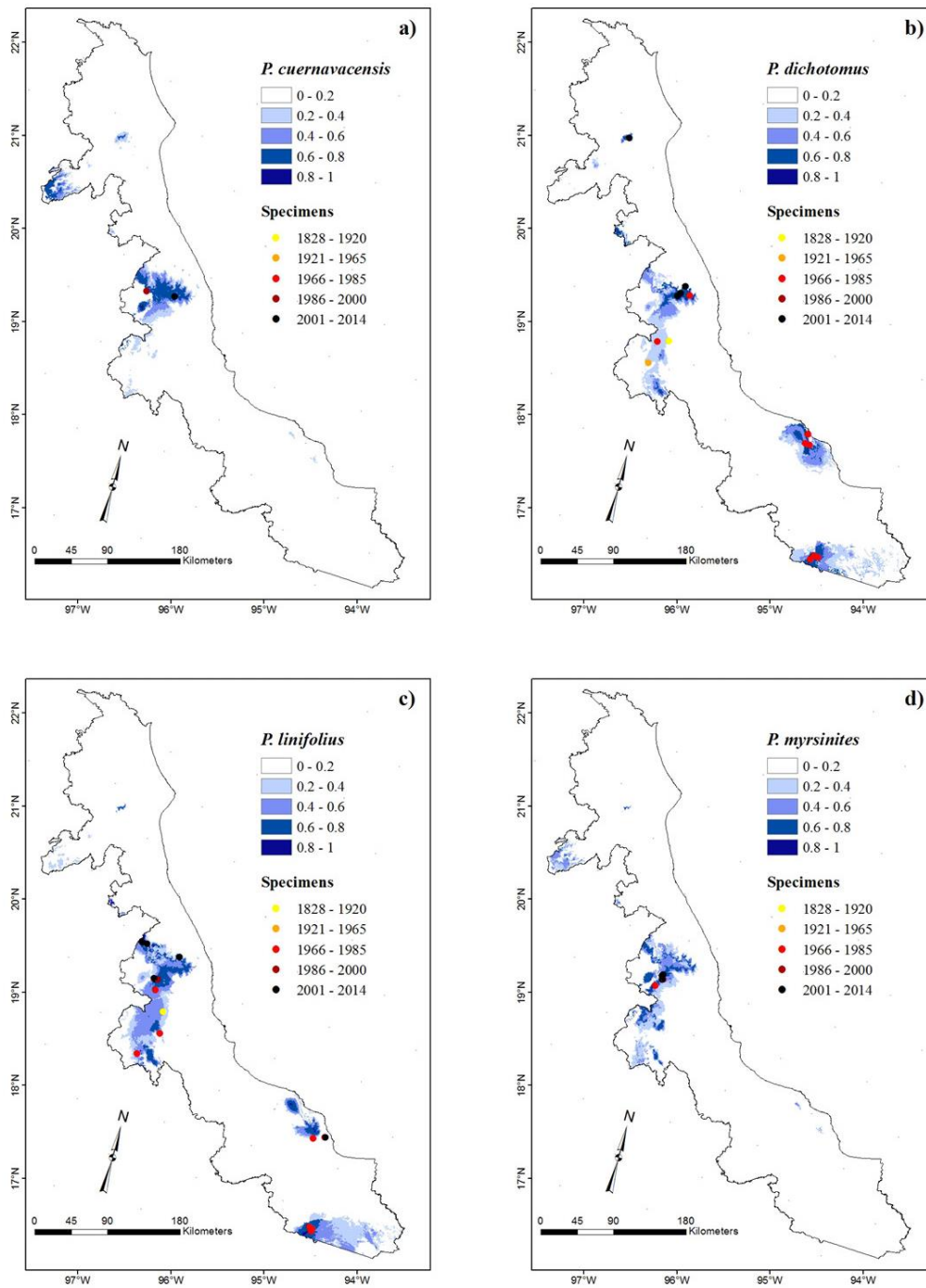
## Results

The obtained information on distribution, ecology and conservation status of all nine *Phlegmariurus* species recorded for the state of Veracruz is given in Appendix 2. These species were mostly distributed in the center (montane zone) and south (Los Tuxtlas and Uxpanapa regions) of the state between elevations of 120 m to 2,500 m, primarily in humid montane forests, but also in tropical humid, oak, pine-oak and *Liquidambar* forests. The municipalities with most collections and species were: San Andrés Tuxtla (30 collections/4 species), Zongolica (18/4), Sotapan (15/5), Tlalnahuayocan (14/4), Acajete (9/5), Yecuatla (7/5) and Hidalgotitlán (7/3).

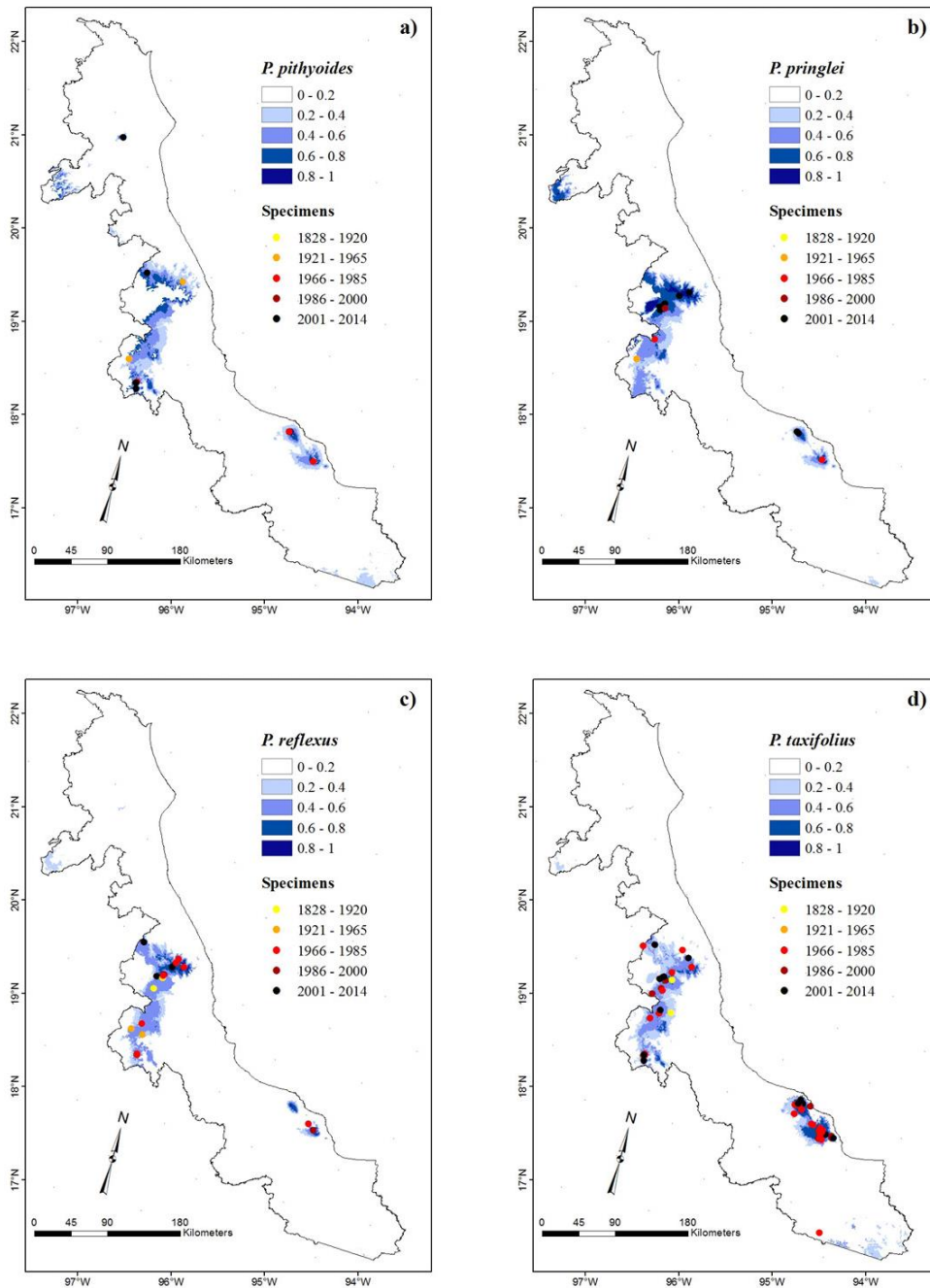
Within the five periods of collection dates, only eight *Phlegmariurus* collections were obtained from historical collectors such as Schiede, Müller, Pringle, Purpus and Barnes between 1828-1920; only six collections were recorded between 1921-1965, of which five were by Copeland in 1938; the period from 1965 to 1985 contains almost half of the collections (80) with the majority collected in the 1980s principally in the Los Tuxtlas region; the period from 1986 to 2000 comprises more than a decade in which only 24 collections were made; 56 collections were recorded between 2001-2014, the majority of these by the authors and/or collaborators and most of them collected in the Los Tuxtlas region, specifically on the San Martín Tuxtla volcano and in the vicinity of the Cofre de Perote region in the municipalities of Acajete and Tlalnahuayocan.

The potential distributions of all eight species analyzed correspond to the central montane region of the state, the Los Tuxtlas region and the Sierra de Huayacocotla (Fig. 3 and 4). The predictive accuracy of the models generated for all species was high, with AUC values ranging between 0.960-0.995. The three variables that best explain the presence of all these *Phlegmariurus* species were: precipitation in wettest month, altitude, and mean temperature of wettest quarter. According to the IUCN [24, 25] classification, *Phlegmariurus dichotomus*, *P. linifolius*, *P. pithyoides*, *P. pringlei*, and *P. taxifolius* are classified as vulnerable (VU), whereas *P. cuernavacensis*, *P. myrsinites*, and *P. reflexus* are endangered (EN) in Veracruz, principally as a result of its restricted distribution as well as habitat loss and fragmentation. Finally, *P. orizabae* is classified as critically endangered (CR), as it is only known from a single specimen collected over a century and a half ago.





**Fig. 3. Current and potential distribution of *Phlegmariurus* species in Veracruz, Mexico: a) *P. cuernavacensis*, b) *P. dichotomus*, c) *P. linifolius*, d) *P. myrsinites*. The probability of presence as predicted by the Maxent models (0-1) is depicted. Specimen locations are indicated by dots, coded according to collection periods.**



**Fig. 4. Current and potential distribution of *Phlegmariusus* species in Veracruz, Mexico: a) *P. pithyoides*, b) *P. pringlei*, c) *P. reflexus*, d) *P. taxifolius*. The probability of presence as predicted by the Maxent models (0-1) is depicted. Specimen locations are indicated by dots, coded according to collection periods.**

## Discussion

Our study focused at a regional level in which the conservation status of *Phlegmariurus* was evaluated with available information for the state of Veracruz only; some species considered as threatened in this study could have a different conservation status or even be abundant in other regions or geographical scales. Nonetheless, the status we assign for Veracruz is related to the severe deforestation problem [12], as it is among the states with the highest deforestation nationwide [38]. In addition, we note that the state is located within latitudes where some species reach their northernmost distribution and thus are at the margins of their global range [10]. Range limits are often determined by the unavailability of suitable habitats, which may cause smaller population sizes [44].

*Phlegmariurus* is represented by nine species in Veracruz, of which, according to our analysis, all are found in some category of risk according to IUCN [24, 25] criteria at the regional level. The principal reasons for the strong threat are the continuous loss and fragmentation of natural habitats, such as humid montane, pine-oak and tropical humid forests [12, 39, 40]. Our results are even more severe compared to those obtained by Krömer et al. [45] for 18 grammitid ferns that occur in Veracruz, of which 72% belong to a threatened category. Also, according to Tejero-Díez et al. [11], all *Phlegmariurus* species in Veracruz should be considered as threatened or endangered; to reach this conclusion, they utilized criteria based on Mexican legislation in order to classify conservation status. However, their results are based mainly on a study conducted over two decades ago by Palacios-Ríos [22]. Tejero-Díez et al. [46] reaffirmed the need to conduct studies to evaluate conservation status of Mexican ferns and lycophytes in general. This is particularly urgent because of the knowledge gaps for this important plant group, reflected in the Mexican legislation (NOM-059-SEMARNAT-2010) for protection of flora and fauna, which includes mostly tree ferns and only one of the 13 *Phlegmariurus* species in Mexico.

With respect to its municipal distribution and vegetation types, the species evaluated are only found in 38 of the 212 municipalities of the state, located mainly in the central montane region and Los Tuxtlas in the southeast, with San Andrés Tuxtla the municipality having the most collected specimens (30). Most of the humid montane forests within Veracruz occur in these regions, which meet the preference of *Phlegmariurus* species for temperate-humid zones [47], since they require special light conditions and are sensitive to prolonged dry periods [48]. In other words, the distribution of the genus in Veracruz is mainly determined by the availability of moist environments with moderate temperatures, found principally in humid montane forests at medium elevations (1,000 to 2,500 m), meeting the most important variables for the presence of the species according to the Maxent model.

The majority of specimens were collected in the 1980s, coinciding with a large effort to conduct an extensive inventory under the Flora de Veracruz program [49]. However, 25% of the recorded *Phlegmariurus* specimens considered in this analysis are recent collections (2005-2014) acquired by the authors and/or collaborators. These current gatherings are of greater importance for the evaluation of their conservation status, since they confirm the presence of these species in remaining habitats, while about 30% of the older collections (periods i-iv) were made in locations, mainly at the slopes of Cofre de Perote and Pico de Orizaba, which are now deforested by human activities and land-use change during the 1970-1990s [50, 51]. During the period of 1990-2000

between 3.8 and 4.8 % of natural forest vegetation of Veracruz was deforested by the expansion of pasture lands, construction of roads, and urban development [12, 38].

Humid montane forests in Veracruz are also threatened by human population growth, with greater threat intensity in the central montane region [40]. In the case of the Los Tuxtlas region, 59% of forest vegetation cover was lost in the last three decades, despite being located within a Biosphere Reserve [39]. It is important to mention that those areas where *Phlegmariurus* species were found are also considered conservation hotspots in the state based on vegetation cover loss and anthropogenic pressures [12]. The loss of natural vegetation cover that is documented in these three studies directly affects plant diversity, especially of groups sensitive to these changes such as the *Phlegmariurus* genus.

Along with Chiapas and Oaxaca, Veracruz has the most vascular plant diversity of any Mexican state [30, 52], but it also has the highest loss of natural vegetation in the country [38]. In the period between 1984 and 2000, Veracruz lost 36% of its existing forest cover [53]. Presently, less than 8.6% of the original natural vegetation remains in isolated fragments, while the rest of the state is covered by agricultural and pasture land, as well as secondary vegetation [12]. The humid montane forest (the vegetation type associated with most *Phlegmariurus* specimens) is regarded as one of the most threatened ecosystems in Mexico [40, 54], representing approximately 1% of the country's surface area, of which only 0.4% is considered as primary and the rest (0.6%) as secondary vegetation [55, 56].

The reduction of natural habitat for flora in Veracruz has been alarming, and a large number of endemic species in the state are presently threatened by human activity and ecological deterioration [57]. In the case of *Phlegmariurus*, its vulnerability is mainly due to its sensitivity to prolonged dry periods [48], because most of the species are epiphytes and dependent on their host trees. Forest fragmentation directly affects their survival since this type of disturbance leads to drier and warmer microclimates, causing changes in epiphyte composition to more xerotolerant species [17, 19, 58, 59].

The low number of *Phlegmariurus* specimens collected during the 1990s indicates a strong decline in floristic inventories, possibly due to a change in the focus of botanical studies towards more genetic research, resulting in decreased budgets for herbarium work [60]. Despite the fact that Veracruz is considered one of the most well-known states for knowledge of its flora [57], there is still a need to conduct more research in different regions (e.g., Sierra de Huayacocotla and Otontepec in the north and the Uxpanapa region in the south) where detailed floristic studies have not been conducted. As a result, there is still an absence of most *Phlegmariurus* specimens in these particular regions, even though the potential distribution of some species includes them.

Collections in the central montane region of Pico de Orizaba are mostly very old, with most specimens being collected between 1906-1938 and additional collections dating from the 1980s. Since then the landscape of this region has been dramatically changed by human activities, such as the expansion of urban and pasture land [12]. Thus, we classified *P. orizabae* as critically endangered (CR) with only one known collection made in 1854, and we question whether a greater collection effort in this region and other areas with similar vegetation would result in rediscovering this species. It is possible that land-use change and habitat fragmentation in Veracruz may have resulted

in the extirpation of this species in Veracruz. More recent collections (from the 1980s) have been made in neighboring Oaxaca [10].

Another factor to consider in the evaluation of the conservation status of the genus is the harvesting of individuals from the wild for illegal commercialization in local markets. In Veracruz, mainly in the capital region of the state, one can observe the sale of different species for ornamental purposes: *P. taxifolius*, *P. myrsinites*, and *P. pringlei* [20]. In Oaxaca, the use of *P. reflexus* and *P. taxifolius* has been documented for ceremonial purposes during the festivities of Holy Week [21]. Since these harvesting activities are frequent, uncontrolled and unregulated, we believe that they have a strong impact on local populations; however, no studies have quantified these impacts.

### Implications for conservation

In conclusion, habitat loss due to anthropogenic activities, the antiquity of collected specimens, and the lack of botanical studies are the main reasons affecting the evaluation of conservation of the *Phlegmariurus* species in Veracruz. The present study is the first to conduct a detailed evaluation of its conservation status at a regional level. Since most *Phlegmariurus* species from Veracruz occur as epiphytes in natural humid montane forests, they are largely absent from disturbed or secondary habitats. This suggests that human impacts reduce microenvironments that are favorable for their presence and distribution. Consequently, *Phlegmariurus* species seem to be suitable bioindicators for the evaluation of humid montane forest health and biodiversity. Together with other groups, such as filmy and grammitid ferns [17, 45, 61], they may be suitable to detect priority areas for conservation.

We identified significant gaps in knowledge of *Phlegmariurus* distribution in the northern and southern parts of Veracruz, mainly in the Huayacocotla and Uxpanapa regions that are not included in the current protected areas network of Veracruz [62]. This highlights the importance of conducting detailed floristic inventories in order to confirm the potential distribution of several *Phlegmariurus* species and reveal other endemic or endangered plants, which could argue for the creation of new reserves in these regions. In addition to *in situ* conservation, it is important to raise awareness among plant collectors and the public about *Phlegmariurus* and epiphytes in general. Moreover, environmental education, management programs and regulations should be applied in order to promote the sustainable harvest of *Phlegmariurus* as well as discourage their illegal commercialization.

Our results contrast with the national legislation which lists only one species, *P. dichotomus*, as “protected” by law (NOM-059-SEMARNAT-2010) and classified as vulnerable, whereas none of the nine species reported for Veracruz have been previously included in the IUCN Red List [63]. We consider that the Mexican law regarding the protection of biodiversity and list of endangered species [23] is currently incomplete and requires the consideration and integration of studies such as ours, to enable an updated and more complete evaluation of the state of conservation of species of flora in Mexico.

Though *Phlegmariurus* is represented by relatively few species in Veracruz and Mexico, our study could serve as a model for future work in other groups of tropical vascular epiphytes [17, 18, 64]. The lack of knowledge about the distribution of many groups of tropical plants [65], in addition to

the continuing reduction in natural habitat, make it urgent to conduct more floristic studies for conservation purposes in Mexico and other parts of the world.

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**Appendix 1.** Index to the 173 revised collections. The numbers in parentheses refer to the corresponding species: *Phlegmariurus cuernavacensis* (1), *P. dichotomus* (2), *P. linifolius* (3), *P. myrsinites* (4), *P. orizabae* (5), *P. pithyoides* (6), *P. pringlei* (7), *P. reflexus* (8), *P. taxifolius* (9). Acevedo R 186 (3). Acosta P 1676 (9). Alor S s.n. (8). Avendaño R 488 (7). Barnes 103 (8). Beaman 5586, 5699, 5766, 5931 (9); 6227 (7); 6232 (9); 6280 (6); 6410 (9). Blanco F 1 (9); 11 (8). Calzada 126 in part, 1548 (2); 7878 (8); 11261 (3); 11839, 11851, 11987, 12761 (9). Carvajal H 173 (9); 247 (7); 353 (9); 355 (7); 433 (9); 434 (7); 712 (9); 795 (3). Castillo C 13360 (9); 22722 (7). Cedillo T 3210 (9). Cházaro B 2796 (4). Contreras C s.n. (6). Copeland s.n. (2, 7, 8); 161 (8); 162 (6). Dorantes L 2381 (8); 2569 (3); 2682, 2683 (9); 3140 (2); 3415 (3). Durán E 925 (1). Estrada M 987 (9). Flores P s.n. (7, 9, 9); 889 (3); 900 (4); 1014 (9); 1018 (3). Galán s.n. (9). Gallardo H. 3248 (9); 3263 (3). García G s.n. (8,9); 4 (3). Gómez D 122 (9). Gómez P 788 (6). Hernández 1120 (9). Hernández C 2 (9). Hernández H 112, 143 (8). Hietz 803, 809, 818 (9). Krömer 1913 (2); 1936, 2002, 2085 (9); 2248 (6); 2259 (7); 2263, 2338 (9); 2435 (6); 2518 (7); 2830 (9); 2959 (3); 3038 (9); 3248 (6); 3407 (3); 3418 (6); 3419 (9); 3430 (8); 3545 (3); 3626 (6); 3843 (4); 4007 (3). Levy T 24 (9). Lira 7, 20 (9); 138 (8); 178 (9). López V 9a (9). Lorence 3481 (2). Macuixtle Q 1 (9). Mendoza R 1211 (9). Müller s.n.(5). Murrieta 1 (2). Nee 22473 (9). Osorio L 18 (9). Palacios R 3196 (9); 3277 (2); 3410 (8). Pérez L 300 (2); 301 (6). Pringle 8146, 11803 (8). Purpus 1991 (3); 1990 (2); 7763 (9). Ramamoorthy 3363 (9). Ramírez C s.n. (9). Ramírez R 866, 950 (9); 1241 (8); 1350 (6); 1354 (9); 1381 (2). Riba 442 (9); 928-A (8); 958, 1038 (8); 1099, 1158, 1183 (9). Rincón G 2509 (6). Robledo M 27 (2); 34 (9). Rodríguez A s.n. (9). Romero S 1 (9). Ruíz C 524 (6); 538 (9). Sánchez T s.n. (9). Sangabriel R 31 (4); 33 (7); 81 (4); 82 (9); 92 (7); 172 (8). Santos 508 (3); 509 (9). Schiede 831 (9). Sinaca C 538, 591 (9); 650 (2); 882 (9). Valdivia 959 (2); 1939 (3). Vázquez B 345 (3). Vázquez T 217 (3); 586 (9); 700 (2); 963 (3); 1920 (9); 2530 (2); 3516 (8); 6570 (1); 6570 BIS (2); 6571 (7); 6835 (3); 6838, 6885, 6887 (2); 6946 BIS (8). Zamora s.n. (9). Zamorano s.n. (9).

**Appendix 2.** Distribution, ecology and conservation status of *Phlegmariurus* in Veracruz, Mexico (Chis: Chiapas; Col: Colima; DF: Distrito Federal; Gro: Guerrero; Hgo: Hidalgo; Jal: Jalisco; Méx: México; Mich: Michoacán; Mor: Morelos; Oax: Oaxaca; Pue: Puebla; Qro: Querétaro; Sin: Sinaloa; SLP: San Luis Potosí; Tab: Tabasco; Tam: Tamaulipas; Ver: Veracruz; following Mickel and Smith [10]).

**1. *Phlegmariurus cuernavacensis* (Underw. & F.E. Lloyd) B. Øllg.,** Phytotaxa 57:14, 2012.

Synonym: *Huperzia cuernavacensis* (Underw. & F.E. Lloyd) Holub, Folia Geobotanica et Phytotaxonomica 20:72, 1985.

Distribution: Mexico (Chis, Gro, Jal, Méx, Mich, Mor, Oax, Sin, Ver), Guatemala, El Salvador.

Representative specimens from Veracruz: Acatlán: M. Vázquez T. 6570 (CIB). Las Minas: C. Durán E. and M. Bielma 925 (MEXU, XAL).

Specimens examined: 2 (2 with geographic coordinates).

Ecology: Pendent epiphyte; in the montane region of central Veracruz in humid montane and pine-oak forests between 1,480 and 1,900 m.

Potential distribution: There is a high probability of finding it in the central montane region -Sierra de Chiconquiaco- and to the north in the Sierra de Huayacocotla (EOO: 5,327.5 km<sup>2</sup>; Fig. 3a). AUC: 0.985.

Conservation status: Endangered (EN) B2ab(ii,iii) in Veracruz. Collected in two localities (AOO: 373.3 km<sup>2</sup>), in the central part of the state in humid montane and pine-oak forests, in highly degraded environments, also not found within any natural protected area, increasing the risk of its survival [12, 40].

**2. *Phlegmariurus dichotomus* (Jacq.) W.H. Wagner,** Novon 3(3):305, 1993. Synonym: *Huperzia dichotoma* (Jacq.) Trevis., Atti della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturali (in Milano; di Milano) 17:248, 1874.

Distribution: USA, Mexico (Chis, Col, DF, Gro, Oax, Pue, SLP, Tam, Ver), Guatemala, Belice, Honduras, El Salvador, Nicaragua, Costa Rica, Panama; Granada and The Antilles; Colombia, Venezuela, Trinidad and Tobago, Guayana Francesa, Ecuador, Galapagos, Peru, Brasil, Bolivia, Paraguay.

Representative specimens from Veracruz: Acatlán: M. Vázquez T. 6570BIS (CIB). Catemaco: F. Ramírez R. 1381 (XAL). Chiconquiaco: M. Palacios R. 3277 (XAL). Fortín?: E. B. Copeland s.n. (MEXU). Hidalgotitlán: P. Valdivia Q. 959 (MO). Huatusco: J. Robledo M. 27 (ENCB). Jesús Carranza: M. Vázquez T. et al. 700 (UAMIZ). Landero y Coss: M. Vázquez T. 6887 (CIB). San Andrés Tuxtla: S. Sinaca C. and F. Chigo S. 650 (MEXU, EBT). Tancoco: R. Pérez L. 300 (XAL). Tlacotepec?: C. A. Purpus 1990 (UC). Yecuatla: M. Vázquez T. 6838 (CIB).

Specimens examined: 20 (18 with geographic coordinates).

Ecology: Pendent epiphyte, in the central montane, Pico de Orizaba, and Los Tuxtlas regions, with one recorded specimen for the Sierra de Otontepec to the north, in humid montane and tropical humid forests, between 120 and 1,900 m.

Potential distribution: A high probability exists of finding it in the central montane, Pico de Orizaba, as well as in the Uxpanapa region in the southeast (EOO: 10,820.4 km<sup>2</sup>; Fig. 3b). AUC: 0.973.

Conservation status: Vulnerable (VU) B1ab(ii,iii)+B2ab(ii,iii) in Veracruz. Collected in nine localities (AOO: 628.0 km<sup>2</sup>), in the center and south of the state in humid montane and tropical humid forests. Habitats in three of the localities have suffered from severe loss and transformation to agricultural land [12, 39, 40]; however, recently collected specimens were found in the nuclear zone of the Los Tuxtlas Biosphere Reserve, protecting the species in a way.

**3. *Phlegmariurus linifolius* (L.) B. Øllg.**, Rodriguésia 63(2):480, 2012. Synonym: *Huperzia linifolia* (L.) Trevis., Atti della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturali (in Milano; di Milano) 17:248, 1874 (Fig. 2e).

Distribution: Mexico (Chis, Gro, Oax, Pue, Tab, Ver), Guatemala, Belice, Honduras, El Salvador, Nicaragua, Costa Rica, Panama; Granada and The Antilles; Colombia, Venezuela, Trinidad and Tobago, Suriname, Ecuador, Brasil, Bolivia.

Representative specimens from Veracruz: Acajete: C. Carvajal H. 795 (CIB). Atoyac: R. Acevedo R. and R. Acosta P. 186 (MEXU). Atzalan: T. Krömer et al. 3545 (MEXU, UC, SEL). Hidalgotitlán: J. Dorantes L. et al. 2569 (MO). Pajapan: T. Krömer and E. Otto 2959 (EBT, MEXU, SEL, UC, XAL). Soteapan: A. Santos 508 (CIB). Teocelo: F. Vázquez B. 345 (CIB). Tlacotepec?: C. A. Purpus 1991 (MO, UC). Tlalnelhuayocan: T. Krömer et al. 4007 (XAL). Uxpanapa: J. Dorantes L. et al. 3415 (UAMIZ). Yecuatla: M. Vázquez T. 6835 (CIB). Zongolica: I. García G. 4 (CORU).

Specimens examined: 20 (19 with geographic coordinates).

Ecology: Pendent epiphyte, in the central montane, Los Tuxtlas and Uxpanapa regions, in humid montane and tropical humid forests, between 110 and 1,800 m.

Potential distribution: There exists a high probability of finding the species in the central montane, Pico de Orizaba and the Los Tuxtlas and Uxpanapa regions in southeast of the state (EOO: 11,789.8 km<sup>2</sup>; Fig. 3c). AUC: 0.971.

Conservation status: Vulnerable (VU) B1ab(ii,iii)+B2ab(ii,iii) in Veracruz. Collected in 12 localities (AOO: 1,744.5 km<sup>2</sup>), half of them realized between 2002 and 2014, in the center and south of the state in humid montane, oak and tropical humid forest. Four of the localities suffered from severe forest cover loss and land use change for agricultural purposes [12, 39, 40]. This species has been observed for sale in local markets. Recent collections exist for the nuclear zone of the Los Tuxtlas Biosphere Reserve in the San Martín Pajapan volcano area, providing some protection to this species.

**4. *Phlegmariurus myrsinites* (Lam.) B. Øllg.**, Phytotaxa 57:17, 2012. Synonym: *Huperzia myrsinites* (Lam.) Trevis., Atti della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturali (in Milano; di Milano) 17:249, 1874 (Fig. 2a).

Distribution: Mexico (Chis, Gro, Oax, Ver), Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica; Colombia, Venezuela, Trinidad and Tobago, Suriname, Ecuador, Brasil, Bolivia.

Representative specimens from Veracruz: Acajete: L. Sangabriel R. 81 (XALU). Tlalnelhuayocan: T. Krömer et al. 3843 (MEXU, XAL). Xico: M. Cházaro B. and L. Robles H. 2796 (XALU).

Specimens examined: 5 (5 with geographic coordinates).

Ecology: Pendent epiphyte, in the central montane regions, in humid montane forest, between 1,630 and 2,020 m.

Potential distribution: There exists a high probability of finding the species in the central montane region, Pico de Orizaba, Sierra de Huayacocotla to the north and Los Tuxtlas in the southeast (EOO: 4,465.0 km<sup>2</sup>; Fig. 3d). AUC: 0.995.

Conservation status: Endangered (EN) B1ab(ii,iii)+B2ab(ii,iii) in Veracruz. Collected in three localities (AOO: 53.6 km<sup>2</sup>), only found in the central montane region of the state in tropical montane forests, a vegetation type with severe pressure from human activity [12, 40], additionally not found within any natural protected area, increasing its risk for survival.

**5. *Phlegmariurus orizabae* (Underw. & F.E. Lloyd) B. Øllg.**, Phytotaxa 57:17, 2012. Synonym: *Huperzia orizabae* (Underw. & F.E. Lloyd) Holub, Folia Geobotanica et Phytotaxonomica 20:75, 1985 (Fig. 2d).

Distribution: Mexico (Chis, Gro, Oax, Ver), Guatemala, Honduras, El Salvador.

Representative specimens from Veracruz: Orizaba: C. Müller s.n. (NY).

Specimens examined: 1 (0 with geographic coordinates).

Ecology: Epiphyte; Pico de Orizaba zone at approximately 1,300 m.

Potential distribution: Only one specimen exists, collected in 1854, making it impossible to model its distribution.

Conservation status: Critically Endangered (CR) B2ab(ii,iii) in Veracruz. Only known from its type locality, in the slopes of the Pico de Orizaba (AOO: 21.0 km<sup>2</sup>), and it has not been collected again in the state for more than a century and a half. Although the region is now highly fragmented, pine-oak forest fragments still remain, and thus it is possible that the species may be found again.

Observations: In the study of Palacios-Ríos [17] there are two collections mentioned under *P. orizabae*: Lira 20 (UAMIZ, XAL) and Nee and Calzada 22530 (F, XAL). However, the first was re-identified as *P. taxifolius*, and the second was not found in any of the above-mentioned herbaria and thus not considered in our analysis.

**6. *Phlegmariurus pithyoides* (Schltdl. & Cham.) B. Øllg.**, Phytotaxa 57:17, 2012. Synonym: *Huperzia pithyoides* (Schltdl. & Cham.) Holub, Folia Geobotanica et Phytotaxonomica 20:76, 1985.

Distribution: Mexico (Chis, Gro, Méx, Oax, Qro, SLP, Tam, Ver), Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica; Granada and The Antilles; Colombia and Venezuela.

Representative specimens from Veracruz: Atzalan: T. Krömer et al. 3418 (UC). Mixtla de Altamirano: Y. Ruíz 524 (XAL). Orizaba?: E. B. Copeland 162 (UC, MEXU). San Andrés Tuxtla: T. Krömer and A. Acebey 2435 (EBT, MEXU, SEL, UC, XAL). Soteapan: F. Ramírez R. and F. Vázquez B. 1350 (XAL). Tancoco: R. Pérez L. 301 (XAL). Yecuatla: A. Gómez P. 788 (MEXU). Zongolica: T. Krömer et al. 3248 (MEXU, UC).

Specimens examined: 13 (12 with geographic coordinates).

Ecology: Pendent and erect epiphyte, in the central montane, Los Tuxtlas and Pico de Orizaba regions, and with one recorded specimen for the Sierra de Otontepec to the north, in humid montane and tropical humid forests, between 150 and 1,650 m.

Potential distribution: There is a high probability of finding the species in the central montane, and the Los Tuxtlas and Uxpanapa regions in the southeast, as well as the Sierra de Huayacocotla to the north (EOO: 9,313.8 km<sup>2</sup>; Fig. 4a). AUC: 0.973.

Conservation status: Vulnerable (VU) B1ab(ii,iii)+B2ab(ii,iii) in Veracruz. Collected in six localities (AOO: 920.5 km<sup>2</sup>), in the center and south of the state in humid montane, oak and tropical humid forests, environments with a lot of anthropogenic pressure, of which two localities are highly fragmented [12, 39, 40]; additionally it has been observed for sale in local markets. Recently collected specimens exist in the nuclear zone of the Los Tuxtlas Biosphere Reserve, on the San Martín Tuxtla volcano, somewhat protecting this species.

**7. *Phlegmariurus pringlei* (Underw. & F.E. Lloyd) B. Øllg.**, Phytotaxa 57:18, 2012. Synonym: *Huperzia pringlei* (Underw. & F.E. Lloyd) Holub, Folia Geobotanica et Phytotaxonomica 20:76, 1985 (Fig. 2b, f).

Distribution: Mexico (Chis, Gro, Hgo, Méx, Mich, Mor, Oax, Ver), Guatemala, Honduras, El Salvador.

Representative specimens from Veracruz: Acajete: C. Carvajal H. 355 (MEXU). Acatlán: M. Vázquez T. 6571 (CIB). Coatepec: G. Castillo C. 22722 (XAL). Huatusco: S. Avendaño R. and G. Castillo C. 488 (UAMIZ). Orizaba?: E. B. Copeland s.n. (UC). Tlalnahuayocan: C. Carvajal H. 434 (MEXU). San Andrés Tuxtla: T. Krömer and A. Acebey 2259 (EBT, MEXU, SEL, UC). Soteapan: J. Beaman 6227 (MEXU).

Specimens examined: 14 (13 with geographic coordinates).

Ecology: Pendent epiphyte; in the central montane and Los Tuxtlas regions in the southeast, in humid montane, oak, pine-oak and tropical dry forests, between 1,450 and 2,000 m.

Potential distribution: There is a high probability of finding the species in the central montane and Pico de Orizaba regions, as well as in Los Tuxtlas in the southeast and the Sierra de Huayacocotla in the northern part of the state (EOO: 9,525.7 km<sup>2</sup>; Fig. 4b). AUC: 0.951.

Conservation status: Vulnerable (VU) B1ab(ii,iii)+B2ab(ii,iii) in Veracruz. Collected in nine localities (AOO: 422.3 km<sup>2</sup>), only in the central montane and Los Tuxtlas regions of the state, in humid montane and tropical humid forests, habitats of the Pico de Orizaba area are highly fragmented [12, 40]; additionally observed on sale in local markets. The majority of the specimens are recent (2002-2012), some of them collected on the slopes of the San Martín Tuxtla volcano, which forms part of the nuclear zone of the Los Tuxtlas Biosphere Reserve.

Observations: In the study of Palacios-Ríos [17] the specimen of S. Avendaño R. and G. Castillo C. 488 (XAL) is identified as *H. tuerckheimii*; however, this name is a synonym of *P. pringlei*.

**8. *Phlegmariurus reflexus* (Lam.) B. Øllg.**, Rodriguésia 63(2):481, 2012. Synonym: *Huperzia reflexa* (Lam.) Trevis., Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturali (in Milano; di Milano) 17:248, 1874.

Distribution: Mexico (Chis, Gro, Hgo, Jal, Méx, Oax, Pue, Ver), Guatemala, Belice, Honduras, El Salvador, Nicaragua, Costa Rica, Panama; Granada and The Antilles; Colombia, Venezuela, Trinidad and Tobago, Ecuador, Perú, Brasil, Bolivia, Paraguay.

Representative specimens from Veracruz: Acajete: L. Sangabriel R. 172 (XALU). Atzalan: T. Krömer et al. 3430 (MEXU, UC). Banderilla: J. I. Calzada 7878 (XAL). Catemaco: R. Lira S. 138 (UAMIZ). Chiconquiaco: R. Riba and B. Pérez G. 958 (UAMIZ). Chocamán: R. Riba and B. Pérez G. 1038 (UAMIZ). Fortín?: E. B. Copeland 161 (MEXU, UC). Jilotepec: V. Hernández H. 112 (XAL). La Perla?: E. B. Copeland s.n. (UC). Miahuatlán: M. Vázquez T. 6946 BIS (CIB). Soteapan: M. Vázquez T. 3516 (CIB). Xalapa: C. Pringle 11803 (MEXU, UC). Xico?: C. Barnes et al. 103 (F). Yecuatla: M. Palacios R. 3410 (XAL). Zongolica: E. Blanco F. 11 (CORU).

Specimens examined: 22 (18 with geographic coordinates).

Ecology: Terrestrial, rarely epiphytic; in the central montane region and Pico de Orizaba mountain in humid montane forests, between 800 and 1,600 m.

Potential distribution: There is a high probability of finding the species in the central montane and Pico de Orizaba regions, as well as in Los Tuxtlas in the southeast of the state (EOO: 5,242.6 km<sup>2</sup>; Fig. 4c). AUC: 0.979.

Conservation status: Endangered (EN) B2ab(ii,iii) in Veracruz. Collected in 15 localities (AOO: 490.31 km<sup>2</sup>), principally in the central montane region and on two occasions in Los Tuxtlas, in humid montane and tropical humid forests, of which seven localities of the central montane region contain highly fragmented habitat converted to agricultural lands [12, 40]. Moreover, only the most recent collections were found on the Santa Marta volcano, in the nuclear zone of the Los Tuxtlas Biosphere Reserve, and the majority of the specimens were collected over two decades ago.



**9. *Phlegmariurus taxifolius* (Sw.) Á. Löve & D. Löve**, Taxon 26(2-3):324, 1977. Synonym: *Huperzia taxifolia* (Sw.) Trevis., Atti della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturali (in Milano; di Milano) 17:248, 1874 (Fig. 2c, f).

Distribution: Mexico (Chis, DF, Gro, Hgo, Jal, Méx, Oax, Pue, Sin, SLP, Tam, Ver), Guatemala, Belice, Honduras, El Salvador, Nicaragua, Costa Rica, Panama; Granada and The Antilles; Colombia, Venezuela, Trinidad and Tobago, Ecuador, Perú, Bolivia.

Representative specimens from Veracruz: Acajete: C. Carvajal H. 353 (MEXU). Atzalan: T. Krömer et al. 3419 (MEXU, SEL, UC). Catemaco: R. Lira S. 178 (MEXU, UAMIZ). Chiconquiaco: R. Riba 442 (UAMIZ). Coatepec: P. Hietz and U. Seifert 803 (XAL). Coscomatepec: R. Hernández C. and R. Trigos 1120 (MEXU). Hidalgotitlán: M. Vázquez T. et al. 586 (UAMIZ, XALU). Huatusco: S. Levy T. 24 (UAMIZ, ENCB). Ixhuacán de Los Reyes: M. Nee 22473 (F, MEXU, MO). Jalacingo: J. Dorantes L. and M. Acosta 2682 (XALU). Jilotepec: M. Palacios R. 3196 (XAL). Mecayapan: T. Krömer and E. Otto 2830 (EBT, MEXU, UC, XAL). Mixtla de Altamirano: Y. Ruíz C. 538 (XAL). Pajapan: G. Castillo C. et al. 13360 (XAL). San Andrés Tuxtla: T. Krömer and A. Acebey 2085 (EBT, MEXU, UC, XAL). Soteapan: R. Riba et al. 1099 (MEXU, UAMIZ, XAL). Tatahuicapan: C. Carvajal H. 712 (CIB). Tlacotepec?: C. A. Purpus 7763 (UC). Tlalnelhuayocan: C. Carvajal H. 433 (MEXU). Xalapa?: C. J. W. Schiede 831 (MEXU). Xico: P. Hietz and U. Seifert 809 (XAL). Yecuatla: M. Vázquez T. 1920 (ENCB). Zongolica: T. Krömer et al. 3038 (MEXU, SEL, UC).

Specimens examined: 76 (74 with geographic coordinates).

Ecology: Pendent epiphyte; in the central montane and Pico de Orizaba regions, as well as Los Tuxtlas and Uxpanapa in the southeast, in humid montane, pine, oak, pine-oak, tropical dry and tropical humid forests, between 150 and 2,250 m.

Potential distribution: There is a high probability of finding the species in the central montane and Los Tuxtlas regions in the southeast (EOO: 9,251.0 km<sup>2</sup>; Fig. 4d). AUC: 0.960.

Conservation status: Vulnerable (VU) B1ab(ii,iii) in Veracruz. Collected in more than 30 localities (AOO: 2,059.0 km<sup>2</sup>), half of the collections realized between 2002 and 2014, in the center and south of the state in a variety of vegetation types and areas of the Los Tuxtlas Biosphere Reserve. Habitats in five of the localities of the central montane region have been severely modified and converted to agricultural land uses [12, 40], whereas half of the rest of the localities are concentrated in the Los Tuxtlas region, which has also suffered forest loss [39]. Moreover, the species has been observed for sale in local markets.