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Leaf morphometry of six Podocarpaceae species from Peru: A contribution to their taxonomic identification

Morfometría foliar de seis especies de Podocarpaceae del Perú: Un aporte a su reconocimiento taxonómico

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Abstract

The present study evaluated the potential use of leaf morphometry for the taxonomic identification of six Podocarpaceae species. We collected botanical samples from 17 forests across five departments in northern, central, and southern Peru (Cajamarca, Pasco, Junín, Apurímac, and Cusco), and we also performed a multivariate comparison of leaf morphometric variables (length, width, thickness, and area). Hierarchical clustering (dendrogram analysis) successfully discriminated the species, grouping localities with the presence of the same species and identifying six clusters. A Principal Component Analysis (PCA) yielded two components (PCs) that explain 96.1% of the variability of the data; PC1 (71%) is associated with leaf length, width, and area, while PC2 is explained

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by leaf thickness. *Podocarpus celatus* and *Podocarpus magnifolius* exhibit wide and long leaves, *Prumnopitys montana* and *Retrophyllum rospigliosii* have small and thin leaves, and *Podocarpus glomeratus* and *Podocarpus oleifolius* have medium-sized leaves. Finally, we present a brief synopsis of the evaluated species identification keys for the evaluated species, based on leaf morphometry, distribution, conservation status, botanical illustrations, and LCDP plates.

Keywords: Conifers; gymnosperms; leaf traits; montane forests; tropical Andes.

Resumen

El presente estudio evaluó el uso potencial de la morfometría foliar para la identificación taxonómica de seis especies de Podocarpaceae. Se recolectaron muestras botánicas de 17 bosques en cinco departamentos del norte, centro y sur del Perú (Cajamarca, Pasco, Junín, Apurímac y Cusco) y se realizó una comparación multivariada de las variables morfométricas foliares (longitud, ancho, grosor y área). El agrupamiento jerárquico (análisis de dendrogramas) permitió discriminar las especies; agrupó localidades con la misma especie e identificó seis conglomerados. Un Análisis de Componentes Principales (ACP) arrojó dos componentes (CP) que explican el 96,1% de la variabilidad de los datos: el CP1 (71%) se asocia con la longitud, el ancho y el área de la hoja, y el CP2 se explica por el grosor de la hoja. *Podocarpus celatus* y *Podocarpus magnifolius* presentan hojas anchas y largas, *Prumnopitys montana* y *Retrophyllum rospigliosii* tienen hojas pequeñas y delgadas, y *Podocarpus glomeratus* y *Podocarpus oleifolius* tienen hojas medianas. Finalmente, presentamos una breve sinopsis de las claves de identificación de las especies evaluadas, basadas en la morfometría foliar, la distribución, el estado de conservación, las ilustraciones botánicas y las láminas LCDP.

Palabras clave: Andes tropicales; bosques montanos; coníferas; gimnospermas; rasgos foliares.

INTRODUCTION

Conifers are a relict group of woody plants with primitive seeds that have persisted for at least 300 million years. These species have a remarkable capacity for adaptation and diversification and are ecologically and economically important globally (Farjon, 2018). Among conifers, Podocarpaceae Endl. (Endlicher, 1847) is the second most diverse family, with 20 genera and more than 200 species (Farjon, 2017; Page, 2019; Khan *et al.*, 2023). It is distributed worldwide in tropical and subtropical mountain ecosystems (Farjon, 2017; Page, 2019). Species of Podocarpaceae have evergreen leaves with widely variable leaf morphometry, which, together with the resin canals, can be used for taxonomic identification (de Laubenfels, 1985; Biffin *et al.*, 2012; Farjon, 2017).

In addition, seed cone characters, such as the structure of the epimatium, ovule number and orientation, and receptacle morphology, are also indispensable for species delimitation, especially in groups with vegetative morphological overlap (Khan & Hill, 2022).

The evaluation of leaf morphometric descriptors allows the rapid and low-cost taxonomic identification of plants that do not have pollen cones and seed cones. For example, Buchholz & Gray (1948a) carried out a taxonomic revision of *Podocarpus* focused on leaf morphometry and anatomy. Similarly, Mill (2015) conducted the updated taxonomic revision of *Podocarpus* using leaf morphometry as a base input for taxonomic differentiation. *Saxegothaea* and *Lepidothamnus* species were also differentiated based on leaf morphometry (Andruchow-Colombo *et al.*, 2024).

In the Neotropics, the family Podocarpaceae comprises 40 species (Dalling *et al.*, 2011; Page, 2019) distributed in six genera: *Podocarpus* L'Hér. ex Pers. (Persoon, 1807), *Prumnopitys* Phil. (Philippi, 1860), *Pectinopitys* C. N. Page (Page, 2019), *Retrophyllum* C. N. Page (Page, 1989), *Saxegothaea* Lindl (Lindley, 1851) and *Lepidothamnus* Phil. (Philippi, 1861). For Peru, however, there is no exhaustive taxonomic review of the Podocarpaceae species nor taxonomic identification keys based on leaf morphometry. For that country, 12 Podocarpaceae species were reported, which are grouped into four genera: *Podocarpus*, *Prumnopitys*, *Retrophyllum* and *Pectinopitys* (Cernusak *et al.*, 2011; Farjon, 2017; Torres Montenegro *et al.*, 2019; Khan *et al.*, 2023a). They are characterized by having broad, uni-nerved and bilaterally or bifacially flattened leaves (Farjon, 2017; Andruchow-Colombo *et al.*, 2024), but they differ in leaf shape, length, width and thickness. These species are distributed throughout the Peruvian Andes, in the ecosystems of Yunga Basimontane, Montane and Altimontane Forests; meso-Andean Relict Forest, Western Slope Montane Relict Forest and Páramo (Ministerio del Ambiente [MINAM], 2019). Those species play a fundamental role in providing ecosystem services to the population (Vicuña-Miñano, 2005). Despite their importance, these species are threatened due to slow growth, extensive historical logging, establishment on infertile soils and difficulty in propagating (Lawes *et al.*, 2007; Cernusak *et al.*, 2011; Mill, 2016; Farjon, 2017). Several species are within some category of threat (Cernusak *et al.*, 2011); consequently, there is a need to generate more information to contribute to their management and conservation.

This research aimed to evaluate the potential use of leaf morphometry for the taxonomic identification of six species of Podocarpaceae collected in Peru. To do this, we compared the evaluated species using leaf morphometry and elaborated a brief taxonomic synopsis, including an identification key of all Podocarpaceae species from Peru, a description of the species, geographic distribution, conservation status, plates and illustrations of the species.

MATERIALS AND METHODS

Study area and sampling

Within the framework of the Project “Clonal production of Ulcumano plus trees from individuals genetically identified by their stem quality and branch insertion”, we conducted samplings in 17 forests that host representative populations of the family Podocarpaceae in Peru. These forests are located in five departments distributed in the north (Cajamarca department), center (Pasco and Junín departments), and south (Cusco and Apurímac departments) areas of the country, at elevations ranging from 1308 to 2980 m (Fig. 1).

We selected a representative tree of vigorous appearance and good phytosanitary condition from each forest, collected three botanical samples, and prepared herbarium specimens (Table 1). Likewise, we recorded height, DBH (diameter at breast height), elevation and geographic coordinates for each tree. Subsequently, the botanical specimens were indexed in the San Ramón INIA Forest Herbarium (HSRI).

Species identification

For the taxonomic treatment, we used the descriptions and illustrations proposed by Farjon (2017), Reynel *et al.* (2006) and Torres Romero (1988), as well as the information from The Gymnosperm Database (2025). Likewise, we compared the botanical samples with samples of other Podocarpaceae species using the digital images from The Field Museum (2025). We verified the validity of the scientific name with the International Plant Names Index [IPNI] (2025), and we obtained information on the type material of each species from Farjon (2017), Mill (2016), Journal STORage [JSTOR] (2025) and Tropicos (Missouri Botanical Garden, 2025).

Leaf morphometry

From each of the 17 herbarium specimens obtained, we selected 30 leaves and measured the following morphometric characteristics: length (cm), width (cm), thickness (mm) and area (cm²) using an electronic caliper and ImageJ (Schneider *et al.*, 2012). We analyzed the data in the statistical programming environment R project (R Core Team, 2022).

We performed a Principal Component Analysis (PCA) to reduce the dimensionality of the leaf morphometric variables and examine whether they allow differentiation between species (Lê *et al.*, 2008; Kassambara & Mundt, 2016). The optimal number of clusters was determined using the *NbClust* package (Charrad *et al.*, 2014).

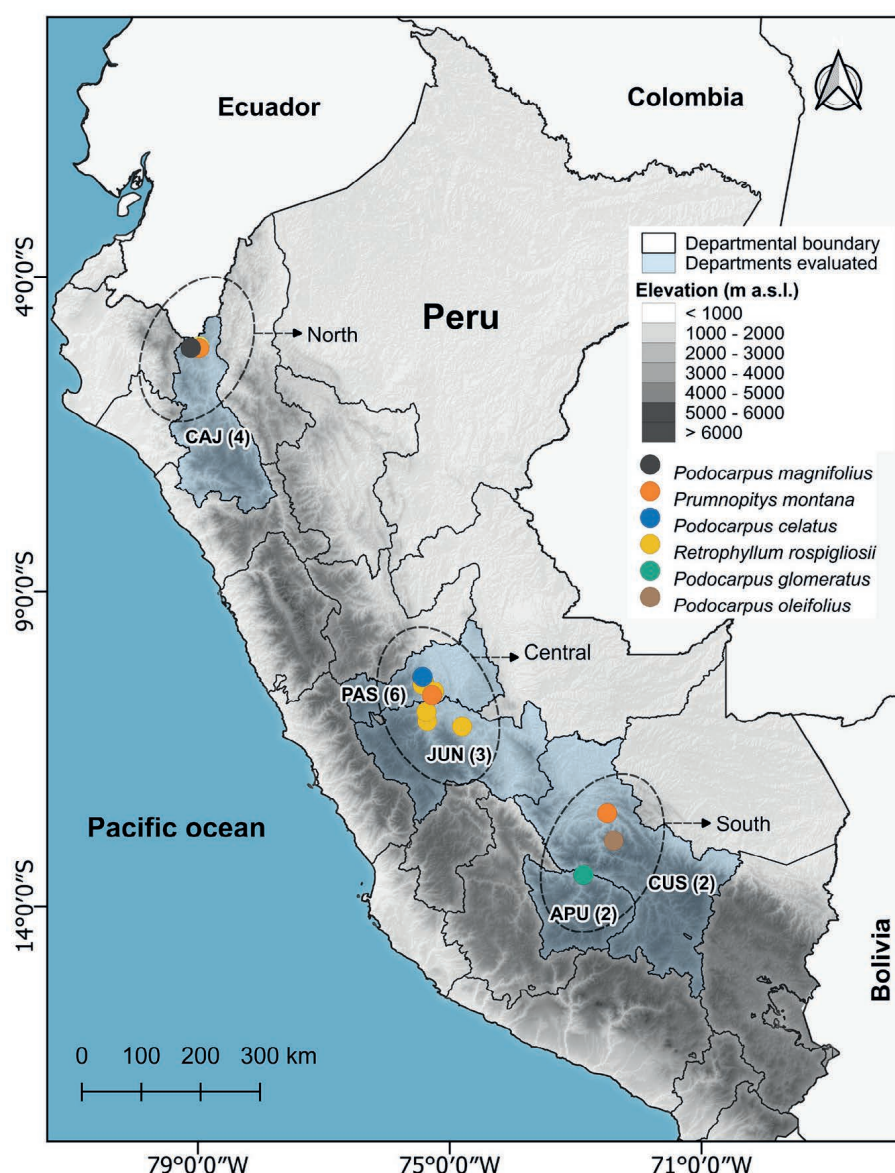


Fig. 1. Podocarpaceae forests assessed in northern, central, and southern Peru. The number in parentheses indicates the number of forests assessed in that department. The initials of the departments were taken from the ISO 3166-2:PE standard.

Fig. 1. Bosques de Podocarpaceae evaluados en el norte, centro y sur del Perú. El número entre paréntesis se indica el número de bosques evaluados en ese departamento. Las siglas de los departamentos fueron tomados de la norma ISO 3166-2:PE.

In addition, to evaluate the grouping of the species based on the evaluation sites, we performed a hybrid hierarchical clustering analysis (Dendrogram) combined with k-means. Finally, we tested statistical differences in foliar characteristics among species using a generalized linear model (GLM) with Gamma distribution since the data did not meet the assumptions of normality and homoscedasticity. Subsequently, we made multiple comparisons of means using Tukey contrasts (Hothorn *et al.*, 2008).

Table 1. List of the six Podocarpaceae species evaluated in Peru. Elev. = Elevation; Depart. = Department, Cons.st. = Conservation status: LC = Least Concern, NT = Near threatened, VU = Vulnerable, CR = Critically Endangered.

Tabla 1. Lista de seis especies de Podocarpaceae evaluadas en Perú. Elev. = Elevación; Depart. = Departamento; Cons.st = Estado de conservación: LC = Preocupación menor; NT = Casi amenazada; VU = Vulnerable; CR = En peligro crítico.

Species	Depart.	District	Elev. (m asl)	Cons. st. IUCN	Cons. st. Peruvian legislation
<i>Podocarpus celatus</i> de Laub.	Pasco	Huancabamba	2130	LC	-
<i>Podocarpus magnifolius</i> J. Buchholz & N.E. Gray	Cajamarca	Tabaconas	2091	LC	NT
<i>Podocarpus oleifolius</i> D. Don	Cusco	Huayopata	2980	LC	CR
<i>Podocarpus glomeratus</i> D. Don	Apurímac	Abancay	2516	NT	NT
		Tamburco	2618		
<i>Prumnopitys montana</i> (Humb. & Bonpl. ex. Willd.) de Laub.	Cajamarca	Chirinos	1882	VU	-
	Pasco	Villa Rica	1583		
	Cusco	Quellouno	1878		
<i>Retrophyllum rospigliosii</i> (Pilg.) C.N. Page	Cajamarca	San Ignacio	1694	VU	NT
		Tabaconas	2094		
	Pasco	Oxapampa	1819		
		Chontabamba	1841		
		Huancabamba	2155		
		Villa Rica	1554		
	Junín	San Ramón	1416		
		Chanchamayo	1308		
		Satipo	1624		

Identification key and botanical description

We followed the terminology proposed by Font Quer (2000) for taxonomic descriptions and comments. The common names were obtained through interviews with local populations. The distribution of the species was based on the reports of Farjon (2017). We obtained the conservation categories from the Red List of Threatened Species of the International Union for Conservation of Nature [IUCN] (2025) and the Categorization of Threatened Species of Wild Flora of Peru, Supreme Decree N° 043-2006-AG (Ministerio de Agricultura [MINAGRI], 2006).

An identification key was developed using leaf morphometric characteristics for 6 of the 10 species of Podocarpaceae reported for Peru. The key was developed by integrating the most discriminating morphometric characteristics supported by previous quantitative analyses.

We also prepared an Illustrated Summary Composition focusing on the morphometric characteristics of the leaves based on the collected herbarium specimens. In addition, we prepared Lankester Composite Dissection Plates (LCDP) from the photographs of the herbarium specimens. These plates display the main characteristics of the leaves and branches, and in some cases include reproductive organs.

RESULTS

Leaf morphometry

We recorded three genera and six species of Podocarpaceae: *Podocarpus celatus* de Laub. (de Laubenfels 1982), *Podocarpus magnifolius* J. Buchholz & N. E. Gray (Buchholz & Gray, 1948b), *Podocarpus oleifolius* D. Don (Lambert *et al.*, 1824), *Podocarpus glomeratus* D. Don (Lambert *et al.*, 1824), *Prumnopitys montana* (Humb. & Bonpl. ex Willd.) de Laub. (de Laubenfels, 1978) and *Retrophyllum rospigliosii* (Pilg.) C. N. Page (Page, 1989). *Retrophyllum rospigliosii* was recorded in three departments and nine districts (political divisions within departments): Pasco (four districts), Junín (three districts) and Cajamarca (two districts). *Prumnopitys montana* was recorded in three departments and three districts: Cajamarca, Pasco and Cusco (one district per department). *Podocarpus glomeratus* was recorded in two districts of the department of Apurímac. The remaining species, *P. celatus*, *P. magnifolius* and *P. oleifolius*, were recorded in only one department: Pasco, Cajamarca and Cusco, respectively (one district per department) (Table 1). The conservation status differed between the IUCN criteria and the Peruvian regulations; however, most species are within a threat category in both frameworks, with *P. montana*, *R. rospigliosii* and *P. oleifolius* being the most threatened (Table 1).

Hierarchical clustering identified and grouped the data into six well-defined clusters, each including all the assessment sites that shared the same species. This result indicates consistent intraspecific leaf morphometric similarity (Fig. 2A). The PCA revealed two components, PC1 and PC2, which explained 96.1% of the total variance (71% and 25.1%, respectively). PC1 is associated with leaf length, width, and area, while PC2 is associated with leaf thickness (Fig. 2B). The comparison of species shows a clear differentiation between *P. celatus* and *P. magnifolius* in terms of leaf length and leaf area; however, they have similar leaf width values (Figs. 2B, 3A-B). In addition, *P. glomeratus* and *P. oleifolius* showed similarities in leaf length, thickness and area but differed in leaf width (Figs. 2B, 3C-D). Finally, *R. rospigliosii* and *P. montana* are characterized by having small leaves (in terms of length, width and area) but differ in leaf thickness (Figs. 2B, 3E-F).

Leaf dimensions were variable among species but showed similarities with the PCA results. *Podocarpus celatus* had the greatest leaf length (12.28 ± 1.45 cm), being almost twice the length of *P. magnifolius* (6.07 ± 0.76 cm), four times greater than that of *P. oleifolius* (3.78 ± 0.77 cm) and *P. glomeratus* (3.07 ± 0.55 cm), and more than seven times greater than that of *P. montana* (1.72 ± 0.21 cm) and *R. rospigliosii* (1.59 ± 0.23 cm). The greatest leaf width was recorded in *P. celatus* (1.25 ± 0.11 cm) and *P. magnifolius* (1.18 ± 0.07 cm), followed by *P. oleifolius* (0.51 ± 0.05 cm) and *R. rospigliosii* (0.39 ± 0.06 cm). The species with the smallest leaf width were *P. glomeratus* (0.30 ± 0.04 cm) and *P. montana* (0.28 ± 0.05 cm).

Leaf area showed a similar pattern to that of leaf length, with *P. celatus* exhibiting the largest leaf area ($11.33 \pm 2.23 \text{ cm}^2$), followed by *P. magnifolius* ($5.12 \pm 0.82 \text{ cm}^2$) and *P. oleifolius* ($1.44 \pm 0.38 \text{ cm}^2$). The smallest leaf area values were those of *P. glomeratus* ($0.75 \pm 0.16 \text{ cm}^2$), *R. rospiglosii* ($0.48 \pm 0.13 \text{ cm}^2$) and *P. montana* ($0.42 \pm 0.11 \text{ cm}^2$). Finally, *P. montana* ($0.66 \pm 0.14 \text{ mm}$) had the greatest leaf thickness (Fig. 4).

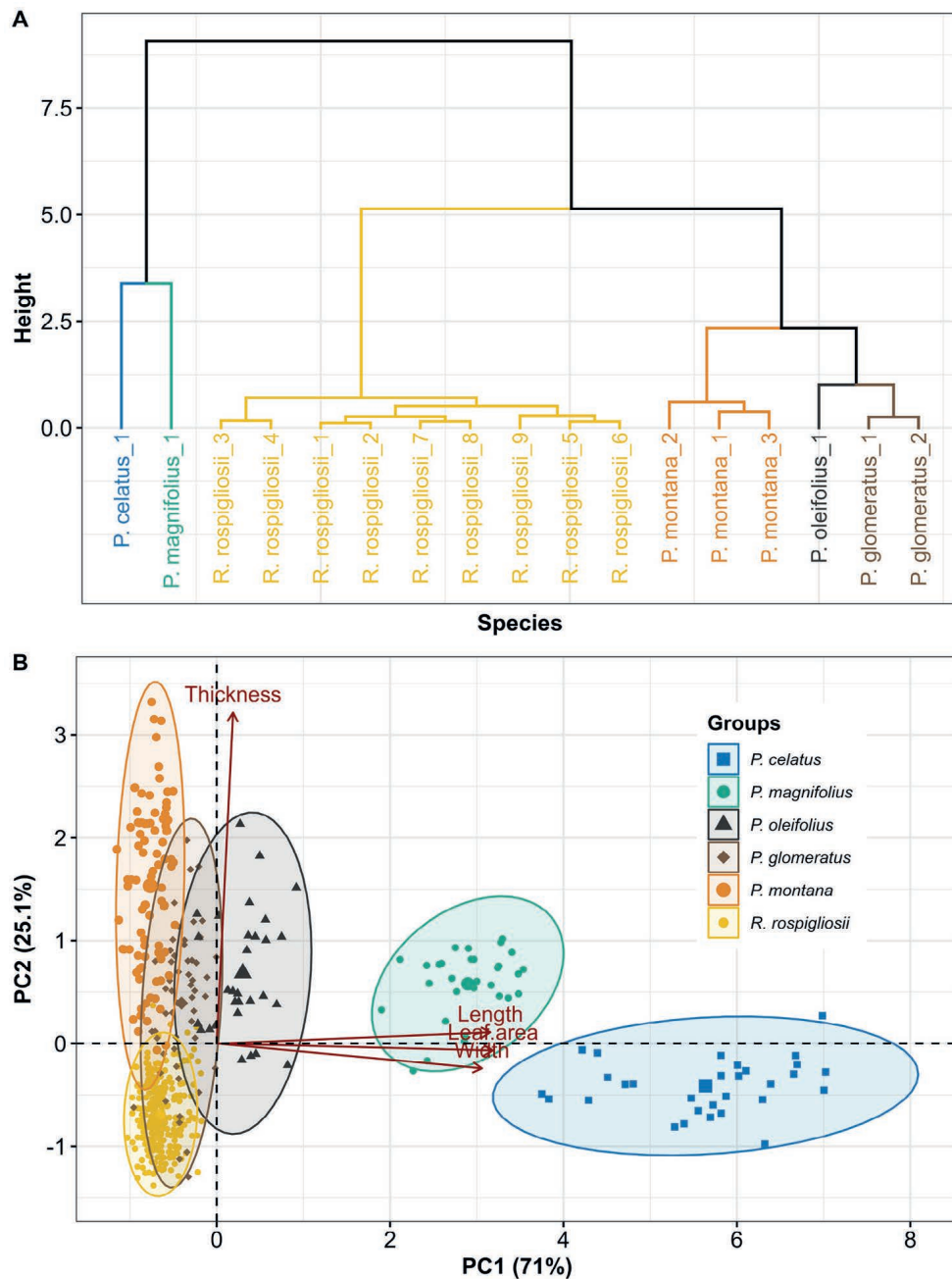


Fig. 2. Multivariate analysis of leaf morphometry of the evaluated Podocarpaceae species. A) Hierarchical clustering. B) Principal Component Analysis.

Fig. 2. Análisis multivariado de la morfometría foliar de las especies de Podocarpaceae evaluadas. A) Agrupamiento jerárquico. B) Análisis de Componentes Principales.

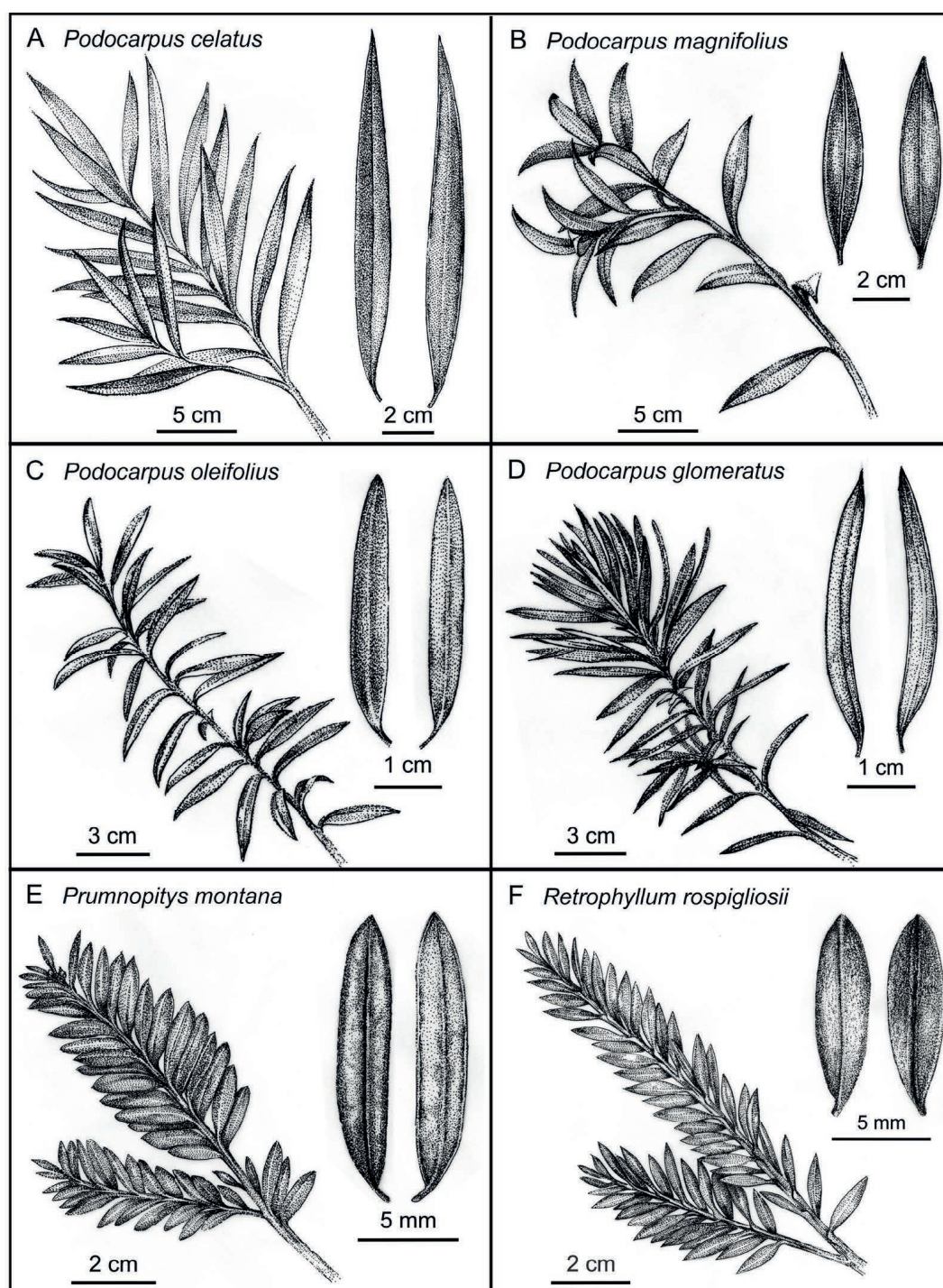


Fig. 3. Illustrated summary composition of the leaf morphometric characteristics of the evaluated Podocarpaceae species. Illustrations by Daniel Galarza Vega (A-F).

Fig. 3. Composición resumida ilustrada de las características morfométricas foliares de las especies de Podocarpaceae evaluadas. Ilustraciones de Daniel Galarza Vega (A-F).

Taxonomic synopsis

Podocarpaceae Endl. (Endlicher, 1847) nom. cons.

Type: *Podocarpus* L'Hér. ex Pers (Persoon, 1807).

Trees or shrubs, dioecious or sometimes monoecious, perennial, semihard to hardwood. Bole cylindrical, dark brown bark, with thin, scaly exfoliating rhytidome of coriaceous and papery appearance. Trunk exhibiting orthotropic, monopodial branching with an irregular evergreen crown. Leaves with a helical arrangement, sessile, simple, of very variable size and shape, with an entire margin, coriaceous, with a single midvein or multiple well-marked parallel veins. Pollen cones simple, axillary or terminal, solitary or grouped, forming compound racemose spike-like units in some genera; pollen scales numerous, imbricate, each with two pollen sacs; pollen with aerial vesicles. Seed cone axillary or terminal, solitary on naked or scaly peduncles, or sessile, composed of many alternate or helically arranged bracts; when mature, it resembles a drupaceous fruit with a dicotyledonous embryo. Seeds generally simple, woody, ovoid, slightly flattened, with hard and sclerified integument and wingless (Farjon, 2017).

Key to six species of Podocarpaceae from Peru using leaf morphometry

- 1 Leaves opposite to subopposite, distichously arranged 2
- 1' Leaves alternate, spirally arranged 3
- 2 Leaves opposite, ovate-lanceolate, 0.99–2.35 cm long $\times$ 0.26–0.53 cm wide, midrib slightly raised on both surfaces, apex acute
..... *Retrophyllum rospigliosii*
- 2' Leaves subopposite, linear and slightly curved above the base, widest above the middle, 1.24–2.16 cm long $\times$ 0.18–0.39 cm wide, midrib grooved adaxially, apex acuminate or mucronate
..... *Prumnopitys montana*
- 3 Leaves linear-lanceolate or oblong-lanceolate, < 4.5 cm long 4
- 3' Leaves elliptic-lanceolate or linear-falcate, $\geq$ 4.5 cm long 5
- 4 Leaves linear-lanceolate, with narrowly acuminate apex that is prickly to the touch, 1.44–4.30 cm long $\times$ 0.23–0.41 cm wide, leaf area of 0.75 cm² *Podocarpus glomeratus*
- 4' Leaves oblong-lanceolate, with an oily sheen on the surface, 2.54–4.64 cm long $\times$ 0.43–0.62 cm wide, leaf area of 1.44 cm²
..... *Podocarpus oleifolius*
- 5 Leaves elliptic-ovoid, 4.68–7.19 cm long $\times$ 1.02–1.31 cm wide, leaf area of 5.12 cm² *Podocarpus magnifolius*
- 5' Leaves lanceolate to linear-falcate, 9.61–14.83 cm long $\times$ 1.04–1.43 cm wide, leaf area of 11.33 cm² *Podocarpus celatus*

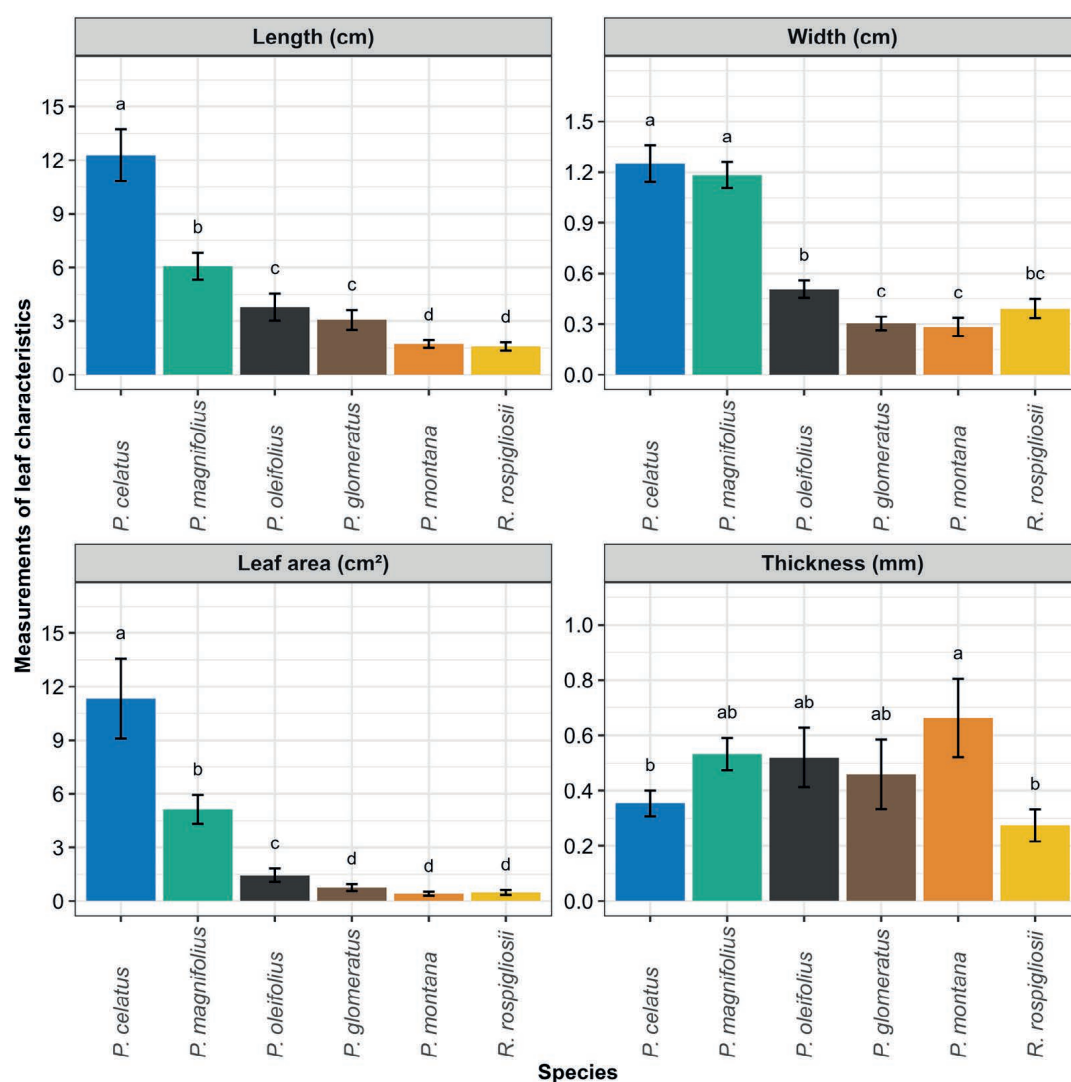


Fig. 4. Bar plot of the leaf morphometric characteristics (length, width, area and thickness) evaluated in Podocarpaceae species. The vertical lines represent $\pm 1SD$ and the letters above the bars represent the results of the Multiple Comparisons of Means (Tukey's contrasts). Different letters indicate statistically significant differences between species ($p < 0.05$).

Fig. 4. Diagrama de barras de las características morfométricas de las hojas (longitud, ancho, área y grosor) evaluadas en las especies de Podocarpaceae. Las líneas verticales representan $\pm 1 DE$ y las letras sobre las barras representan los resultados de las Comparaciones Múltiples de Medias (Contrastes de Tukey). Las letras diferentes indican diferencias estadísticamente significativas entre especies ($p < 0.05$).

1. *Podocarpus celatus* de Laub. (de Laubenfels, 1982)

Type: BOLIVIA. Potosí: Morro, 900 m, January 1866, *R.W. Pearce s.n.* (digital images, lectotype: K!).

Common names: Ulcumano de la puna, ulcumano de altura or romerillo.

Distribution: *Podocarpus celatus* is distributed in evergreen tropical forests of lowlands and low mountains of South America (Venezuela, Colombia, Ecuador, Peru, Brazil and Bolivia). Its altitudinal range is between 130 and 1930 m. In Peru, it is reported for Amazonas, Junín, Loreto, and Puno departments (Farjon, 2017). In this study, it is reported for the department of Pasco.

Description: *Podocarpus celatus* is a tree reaching up to 16 m in height and 45.5 cm in diameter, with a cylindrical bole, fissured trunk, dark brown outer bark, and reddish inner bark. The crown is horizontal and globose, with straight, alternate, striated branches. Leaves alternate spirally; linear-falcate, leathery, margin slightly irregular, $9.61\text{--}(12.38)\text{--}14.83 \times 1.04\text{--}(1.25)\text{--}1.43$, with a thickness of $0.26\text{--}(0.35)\text{--}0.41$ mm, apex acuminate. Male cones amentiform, and the drupaceous seed cones are globose (Fig. 5). *Podocarpus celatus* differs from *P. magnifolius* in having linear-falcate leaves, whereas the latter has elliptical-ovoid leaves. *Podocarpus celatus* also has longer leaves, $4.68\text{--}(6.07)\text{--}7.19$ cm long, a larger leaf area (11.33 ± 2.23 cm² for *P. celatus* vs. 5.12 ± 0.82 cm² for *P. magnifolius*), and thinner leaves ($0.47\text{--}(0.55)\text{--}0.61$ mm for *P. magnifolius*).

Conservation status: IUCN: Least concern (LC), **Peruvian legislation:** Species not categorized as threatened

Examined specimens: PERU. Pasco: Prov. Oxapampa, Distr. Huancabamba, Centro Poblado Navarra, Pastizal alto Papachacra, $10^{\circ}28'52.6''$ S, $75^{\circ}25'48''$ W, 2130 m, 13-VII-2015, *E. Salazar 10* (HSRI!).

2. *Podocarpus magnifolius* J. Buchholz & N. E. Gray (Buchholz & Gray, 1948b)

Type: VENEZUELA. Bolívar: La Gran Sabana, Ptari-Tepui, 1580–1600 m, 10–11-IX-1944, *J.A. Steyermark 59989* (digital images, holotype: F! isotype: ILL! NY!).

Common names: Pino andino or pino de altura.

Distribution: *Podocarpus magnifolius* is distributed in evergreen montane tropical forests in southern Central and South America from 850 m to 2900 m. In Peru, it is recorded in the departments of Huánuco, Pasco and San Martín (Farjon, 2017). In this study, we recorded the species in the department of Cajamarca, Peru.

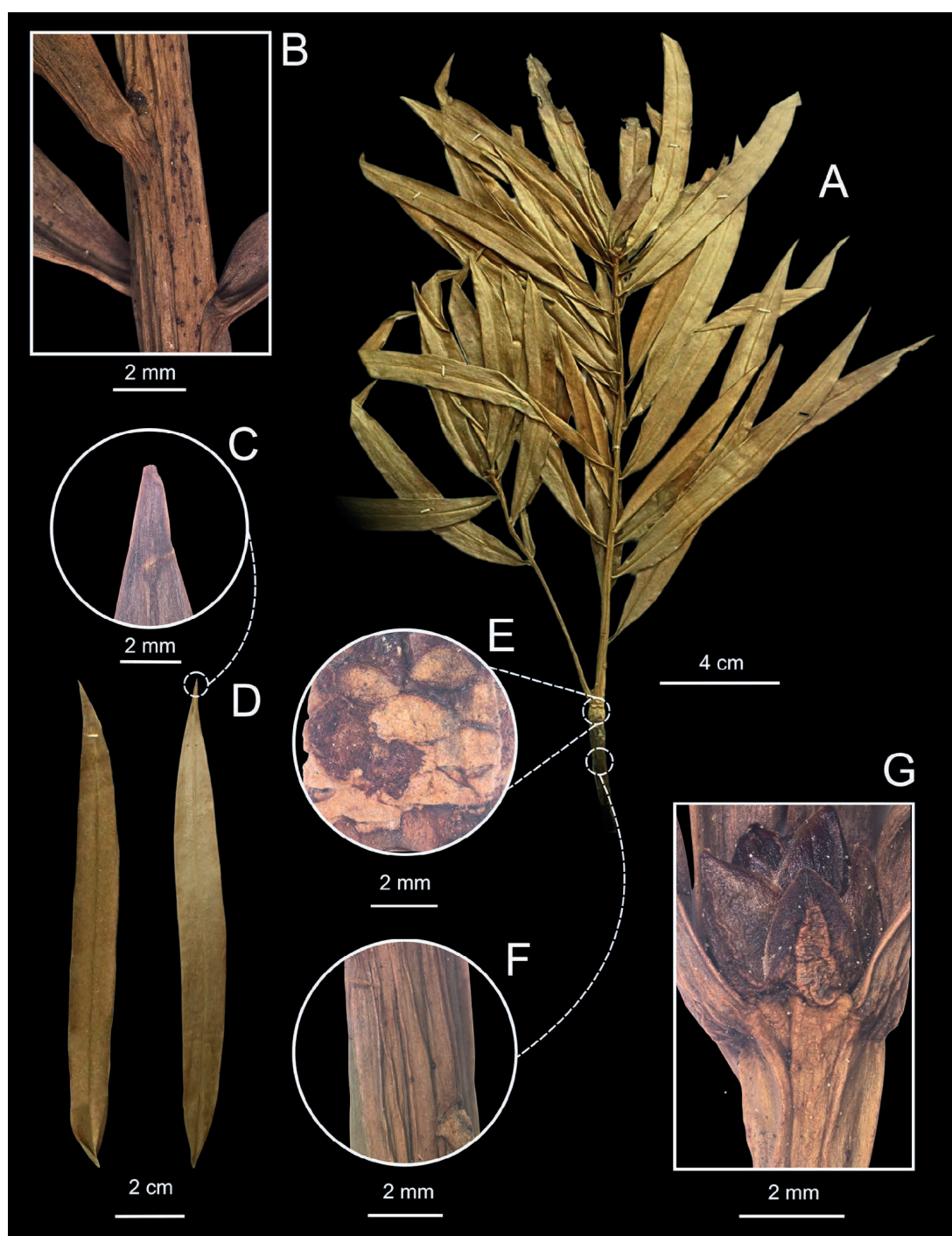


Fig. 5. *Podocarpus celatus*. A) Habit. B) Stem internode. C) Leaf apex. D) Leaf adaxial and abaxial sides. E) Stem base. F) Stem. G) Stem apex. Photographs by Luis David Huayta-Hinojosa and José Antonio Ramírez Peralta. LCDP by L.D.Huayta-Hinojosa. E. Salazar 10 (HSRI!).

Fig. 5. *Podocarpus celatus*. A) Hábito. B) Entrenudo del tallo. C) Ápice de la hoja. D) Caras adaxial y abaxial de la hoja. E) Base del tallo. F) Tallo. G) Ápice del tallo. Fotografías de Luis David Huayta-Hinojosa y José Antonio Ramírez Peralta. LCDP por L.D.Huayta-Hinojosa. E. Salazar 10 (HSRI!).

Description: *Podocarpus magnifolius* is a tree reaching 18 m in height and 35.3 cm in diameter, with a straight cylindrical bole, dark-brown fissured outer bark, and reddish inner bark. The crown is horizontal and globose, with ascending suberect branches. Leaves are arranged alternately in a spiral, large, elliptical-ovoid, with entire margins and a leathery texture. Leaf dimensions are 4.68–(6.07)–7.19 cm in length and 1.02–(1.18)–1.31 cm in width, with a thickness of 0.47–(0.55)–0.61 mm. The apex is acute, and the petiole is twisted. Male cones are amentiform. Seed cones are ellipsoid and drupaceous, with an asymmetrical fleshy receptacle measuring 10–11 cm in length and 5 mm in diameter (Fig. 6). Leaf width of *P. magnifolius* is similar to that of *P. celatus* (1.04–(1.25)–1.43 cm vs. 1.02–(1.18)–1.31 cm).

Examined specimens: PERU. Cajamarca: Prov. San Ignacio, Distr. Tabaconas, Tamborapa, Santuario Nacional Tabaconas Namballe-Unión las Minas, 05°15′24″S, 79°06′47″W, 2091 m, 13-VII-2015, E. Salazar & E. Ccoica 08 (HSRI! ×3).

Conservation status: IUCN: Least concern (LC), **Peruvian legislation:** Near Threatened (NT).

3. *Podocarpus oleifolius* D. Don (Lambert *et al.*, 1824)

Type: PERU.[“in Peruvia ad Pillao et Panao”]: 1778-1788, *Hipólito Ruiz L.* & *José A. Pavón s.n.*, (digital images, lectotype: BM!).

Common names: Romerillo or saucecillo.

Distribution: *Podocarpus oleifolius* is distributed in primary semi-deciduous and evergreen forests in the mountains of Central America (Mexico) and South America (Venezuela, Colombia, Ecuador, Peru and Bolivia). Its altitudinal range is 1200–3300 m (Farjon, 2017). In this study, it was recorded for the department of Cusco.

Description: *Podocarpus oleifolius* is a tree reaching 14.5 m in height and 47 cm in diameter, with a cylindrical bole. The outer bark is thin, dark brown to gray, and very fibrous and slightly wrinkled, while the crown is horizontal and globose, with fissured branches. Leaves are medium-sized, arranged alternately in a spiral, elliptical with entire margins, leathery texture, and an oily appearance. Leaf length is 2.54–(3.66)–4.64 cm, and width is 0.43–(0.50)–0.62 cm, with a thickness of 0.37–(0.51)–0.72 mm. The apex is acute. Seed cones are oval, drupaceous, 8 mm long, and 5 mm in diameter. Male cones are solitary, 15 mm long and 4 mm in diameter, with a sessile, oval peduncle; pollen scales have crenate margins (Fig. 7). *Podocarpus oleifolius* differs from *P. glomeratus* in having wider leaves (0.43–(0.50)–0.62 cm vs. 0.23–(0.30)–0.41 cm in *P. glomeratus*), and *P. glomeratus* has linear-lanceolate leaves with an acute, prickly apex.

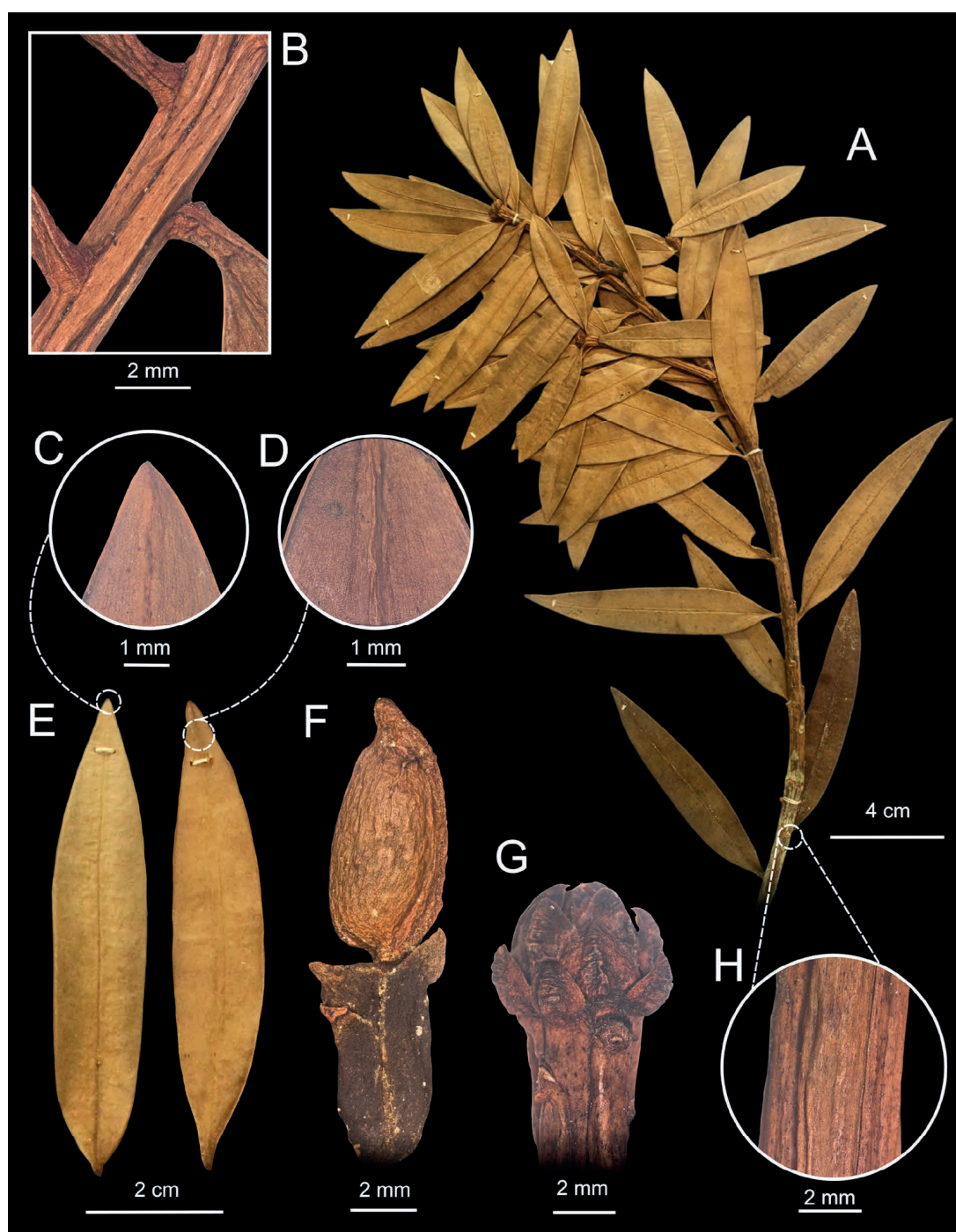


Fig. 6. *Podocarpus magnifolius*. A) Habit. B) Stem internode. C) Leaf apex. D) Central vein on the leaf abaxial side. E) Adaxial and abaxial leaf sides. F) Seed cone. G) Stem apex. H) Stem. Photographs by Luis David Huayta-Hinojosa and José Antonio Ramírez Peralta. LCDP by L.D.Huayta-Hinojosa. E. Salazar & E. Ccoica 08 (HSRI!).

Fig. 6. *Podocarpus magnifolius*. A) Hábito. B) Entrenudo del tallo. C) Ápice de la hoja. D) Nervadura central en la cara abaxial de la hoja. E) Caras adaxial y abaxial de la hoja. F) Cono semillero. G) Ápice del tallo. H) Tallo. Fotografías de Luis David Huayta-Hinojosa y José Antonio Ramírez Peralta. LCDP por L.D.Huayta-Hinojosa. E. Salazar & E. Ccoica 08 (HSRI!).

Conservation status: IUCN: Least Concern (LC), **Peruvian legislation:** Critically Endangered (CR).

Examined specimens: PERU. Cuzco: Prov. La Convención, Distr. Huayopata, Tamborapa, San Luis, 13°04'47''S, 72°23'37''W, 2980 m, 14-IX-2017, Aguirre L. & E. Ccoica 08 (HSRI! 00524 ×3).

4. *Podocarpus glomeratus* D. Don (Lambert et al., 1824)

Type: PERU. Unknown location: 1778–1788, Hipólito Ruiz L. & José A. Pavón s.n., (holotype: BM!).

Common names: Intimpa, huampo, romerillo or pumatakana.

Distribution: *Podocarpus glomeratus* is distributed in sub-Andean and high mountain forests and shrublands in the Andes of Ecuador, Peru and Bolivia, at elevations between 1800 m and 3600 m (Farjon, 2017). In Peru, it has been recorded in Huánuco and Apurímac (as in this study).

Description: *Podocarpus glomeratus* is a tree or shrub reaching up to 11 m in height and 47 cm in diameter. The bole is generally cylindrical, with fissured to cracked dark brown outer bark and creamy pink inner bark. The crown is globose, with branches emerging from the upper third of the tree. Leaves are arranged alternately in a spiral, medium-sized, simple, and linear-lanceolate in shape. The leaf margins are entire, with a leathery texture and an acute, prickly apex. Leaf length is 1.44–(3.07)–4.30 cm, width is 0.23–(0.30)–0.41 cm, and thickness is 0.16–(0.45)–0.70 mm. Male cones are grouped in clusters of 4 or 5, resembling catkins, born on a peduncle. Male cones length is 6.8–(9.2)–13 mm, with a diameter of 1.1–(1.3)–1.6 mm. Seed cones are drupaceous, spherical, with a fleshy receptacle, 5–6 mm in length and 4–5 mm in diameter (Fig. 8).

Conservation status: IUCN: Near Threatened (NT), **Peruvian legislation:** Near Threatened (NT).

Examined specimens: PERU. Apurímac: Prov. Abancay, Distr. Tamburco, 13°37'19''S, 72°52'23''W, 2618 m, 13-IX-2017, Aguirre L. & E. Ccoica 05 (HSRI! 00521 ×2). Apurímac: Prov. Abancay, Distr. Abancay, Loc. Abancay, 13°37'39''S, 72°52'42''W, 2516 m, 13-IX-2017, Aguirre L. & E. Ccoica 01 (HSRI! 00517).

5. *Prumnopitys montana* (Humb. & Bonpl. ex Willd.) de Laub. (1978, p. 189).

Type: PERU. Unknown location: Bonpland A.ŷ. & A. von Humboldt s.n., (digital images, holotype: P!).

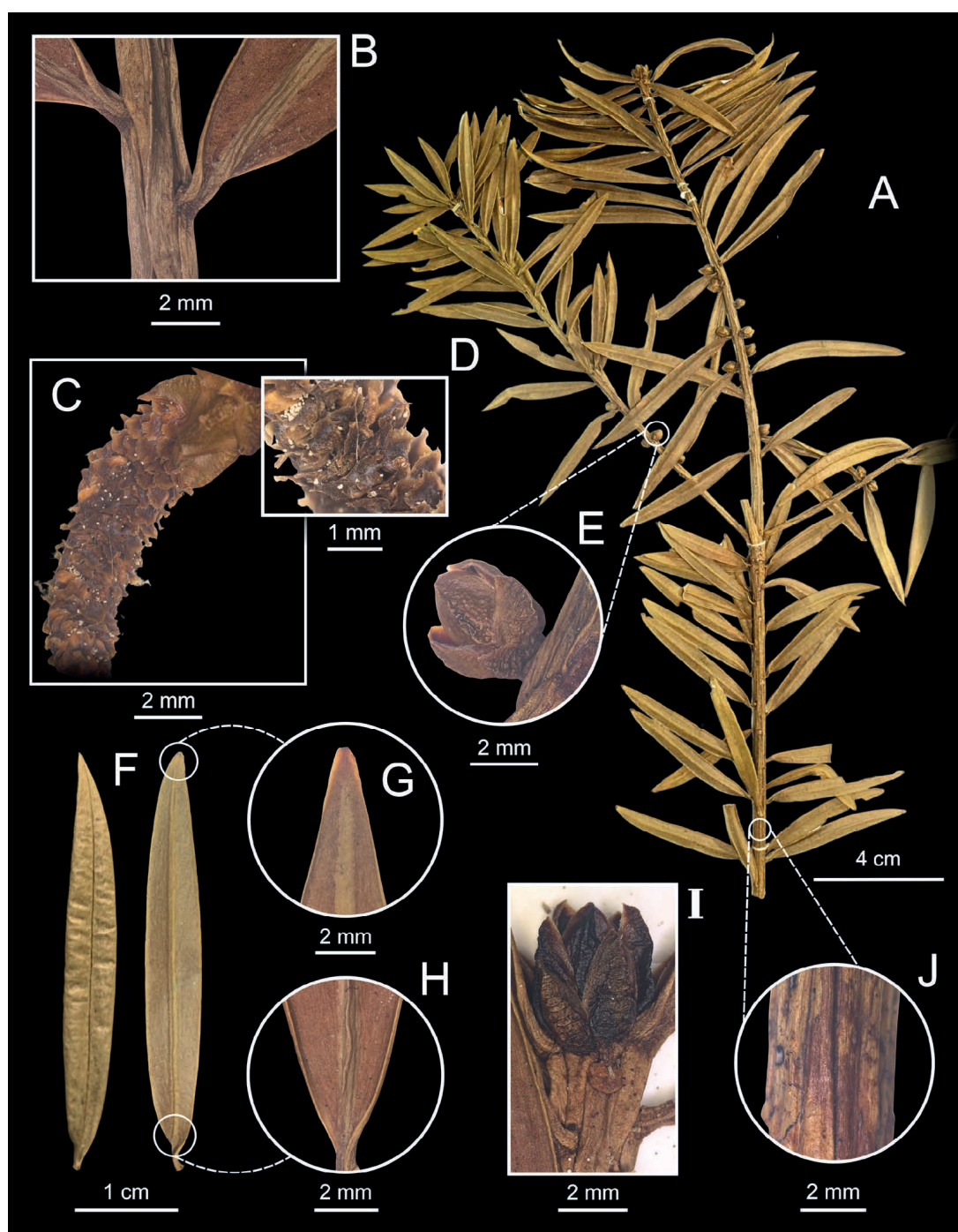


Fig. 7. *Podocarpus oleifolius*. A) Habit. B) Stem internode. C and D) Pollen cone. E) Pollen cone bud. F) Adaxial and abaxial leaf sides. G) Leaf apex (abaxial side). H) Leaf base (abaxial side). I) Stem apex. J) Stem. Photographs by Luis David Huayta-Hinojosa and José Antonio Ramírez Peralta. LCDP by L.D.Huayta-Hinojosa. Aguirre L. & E. Ccoica 08 (HSRI!).

Fig. 7. *Podocarpus oleifolius*. A) Hábito. B) Entrenudo del tallo. C y D) Cono polínico. E) Botón del cono polínico. F) Caras adaxial y abaxial de la hoja. G) Ápice de la hoja (cara abaxial). H) Base de la hoja (cara abaxial). I) Ápice del tallo. J) Tallo. Fotografías de Luis David Huayta-Hinojosa y José Antonio Ramírez Peralta. LCDP por L.D.Huayta-Hinojosa. Aguirre L. & E. Ccoica 08 (HSRI!).

Common names: Diablo fuerte, romerillo hembra, tarco.

Distribution: *Prumnopitys montana* is distributed in the high mountain forests and scrublands of the Andean regions of Colombia, Ecuador, Peru and Venezuela. Elevation ranges from 1500 to 3600 m (Farjon, 2017). This study recorded the species in the departments of Cajamarca, Pasco and Cusco, Peru.

Description: *Prumnopitys montana* is a tree reaching up to 44.7 m in height and 102 cm in diameter, with a cylindrical bole that tapers slightly and that has buttresses at the base. The outer bark is gray and peels off in rigid plates, while the inner bark is whitish. The crown is globose, and the branches are straight and striated. The leaves are alternate, subsessile, distichous, oblong-sigmoid, entire, leathery, with a mucronate apex and an almost flat midrib on the adaxial side. Leaf 1.24–(1.72)–2.16 cm in length and 0.18–(0.28)–0.39 cm in width, with a thickness of 0.38–(0.66)–0.95 mm. Numerous male cones are found along the rameal axis, averaging 4.24 cm in length. Seed cone is drupaceous, with a small apiculate ridge and a diameter of up to 10 mm. (Fig. 9). *Podocarpus montana* is similar to *R. rospiglosii* in having small distichous leaves (0.99–(1.59)–2.35 cm × 0.26–(0.39)–0.53 cm in *R. rospiglosii*), but they differ in leaf shape (oblong-sigmoid in *P. montana* vs lanceolate in *R. rospiglosii*)

Conservation status: IUCN: Vulnerable (VU), **Peruvian legislation:** Species not categorized as threatened.

Examined specimens: PERU. Cajamarca: Prov. San Ignacio, Distr. Chirinos, El Corazón, 05°15'42"S, 78°58'40"W, 1882 m, 19-III-2018, *E. Salazar & E. Ccoica 01* (HSRI! 00541 x2). Pasco: Prov. Oxapampa, Distr. Villa Rica, Loc. Oconal, 10°46'26"S, 75°16'47"W, 1583 m, 27-V-2015, *E. Salazar 09* (HSRI! 009). Cusco: Prov. La Convención, Distr. Quellouno, Loc. Tarco, 12°38'48"S, 72°29'54"W, 1878 m, 12-XII-2017, *E. Salazar 55* (HSRI! 0539).

6. *Retrophyllum rospiglosii* (Pilg.) C.N.Page (Page, 1989)

Type: PERU. Pasco: Oxapampa, Oxapampa, *N. Esposto 556* (holotype: USM!).

Common names: Ulcumano or Romerillo macho.

Distribution: *Retrophyllum rospiglosii* is distributed in the montane tropical forests of Venezuela, Colombia, Ecuador and Peru. Elevation ranges from 1500 m to 3300 m (3750 m in Colombia and Peru). In this study, it was recorded for the departments of Cajamarca, Pasco and Junín, Peru.

Description: *Retrophyllum rospiglosii* is a tree reaching up to 46 m tall and 128 cm in diameter, with a smooth and cylindrical trunk. The outer bark is brown and peels off in papery plates, while the inner bark is yellowish.

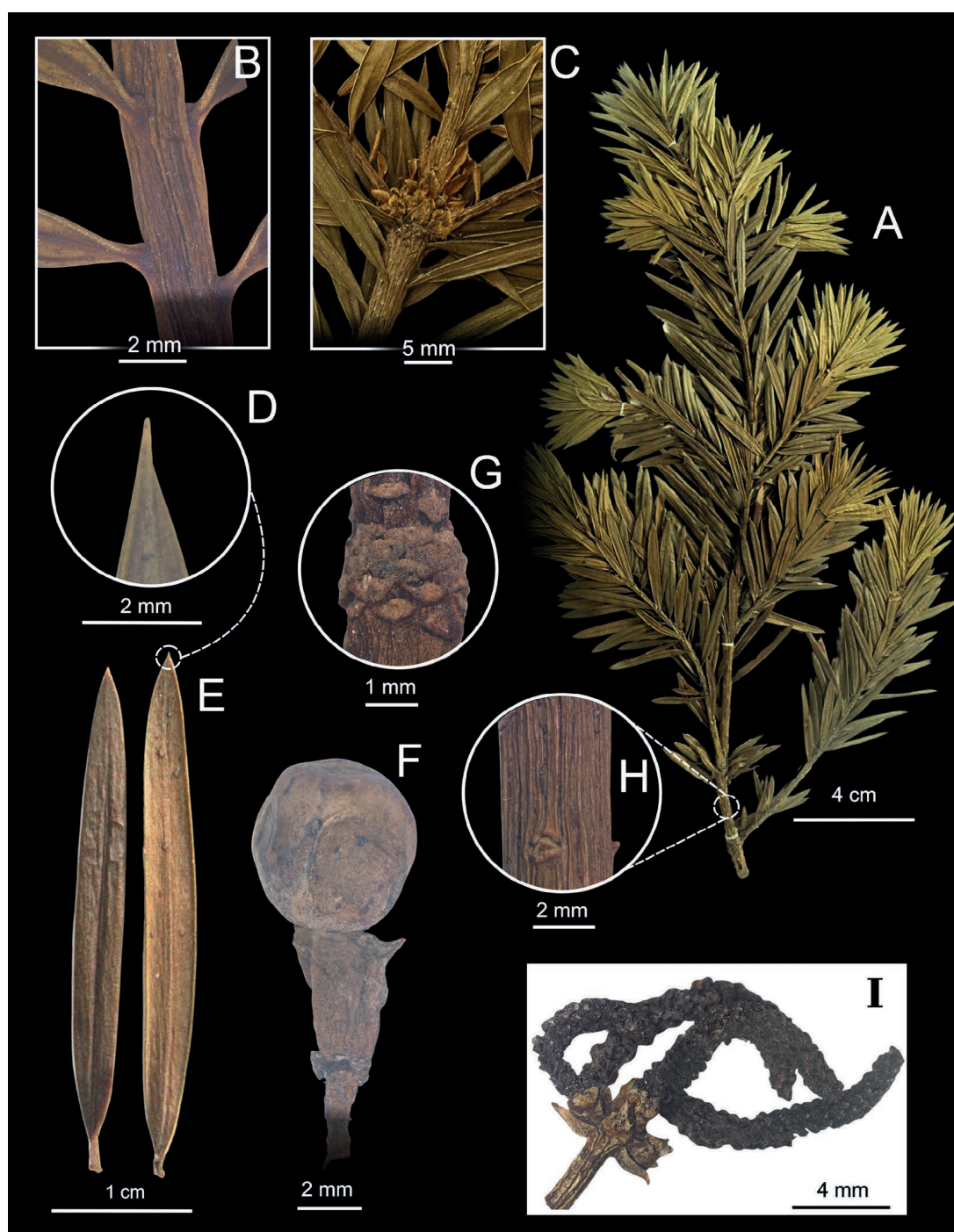


Fig. 8. *Podocarpus glomeratus*. A) Habit. B and C) Stem internode. D) Leaf apex (abaxial side). E) Adaxial and abaxial leaf sides. F) Seed cone. G) Stem base. H) Stem. I) Pollen cone. Photographs by Luis David Huayta-Hinojosa and José Antonio Ramírez Peralta. LCDP by L.D.Huayta-Hinojosa. Aguirre L. & E. Ccoica 05 (HSRI!).

Fig. 8. *Podocarpus glomeratus*. A) Hábito. B y C) Entrenudo del tallo. D) Ápice de la hoja (cara abaxial). E) Caras adaxial y abaxial de la hoja. F) Cono semillero. G) Base del tallo. H) Tallo. I) Cono polínico. Fotografías de Luis David Huayta-Hinojosa y José Antonio Ramírez Peralta. LCDP por L.D.Huayta-Hinojosa. Aguirre L. & E. Ccoica 05 (HSRI!).

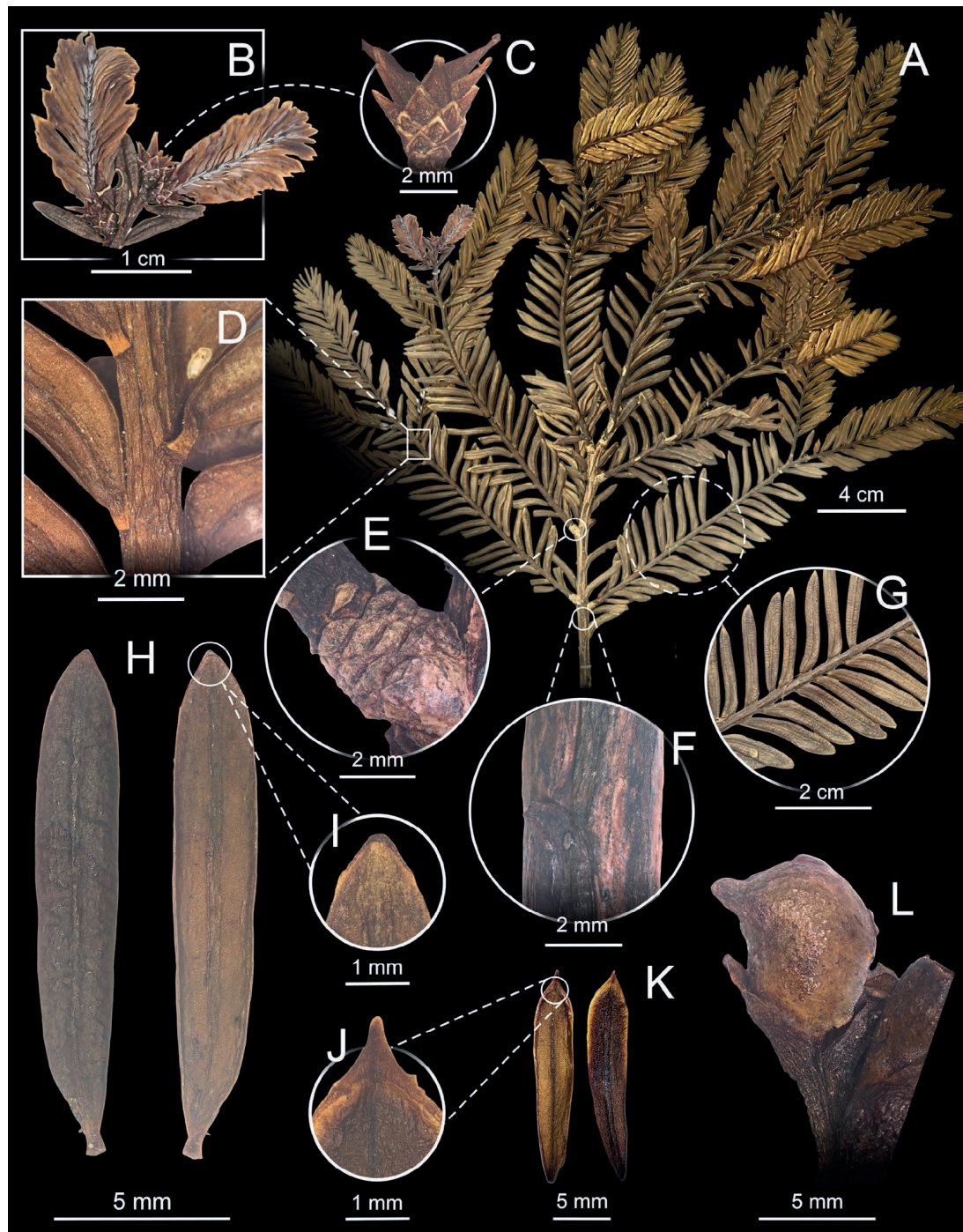


Fig. 9. *Prumnopitys montana*. A) Habit. B) Apex and juvenile leaves. C) Base of juvenile leaves. D) Internode. E) Base of branches. F) Stem. G) Leaves. H) Adaxial and abaxial of the leaf sides. I) Leaf apex. J) Juvenile leaf apex. K) Abaxial and adaxial sides of the juvenile leaf. L) Seed cone. Photographs by Luis David Huayta-Hinojosa and José Antonio Ramírez Peralta. LCDP by L.D.Huayta-Hinojosa. E. Salazar 09 (HSRI!)

Fig. 9. *Prumnopitys montana*. A) Hábito. B) Ápice y hojas juveniles. C) Base de las hojas juveniles. D) Entrenudo. E) Base de las ramas. F) Tallo. G) Hojas. H) Caras adaxial y abaxial de la hoja. I) Ápice de la hoja. J) Ápice de la hoja juvenil. K) Caras adaxial y adaxial de la hoja juvenil. L) Cono semillero. Fotografías de Luis David Huayta-Hinojosa y José Antonio Ramírez Peralta. LCDP por L.D.Huayta-Hinojosa. E. Salazar 09 (HSRI!).

The leaves are opposite, sessile, distichous, lanceolate, entire, and flat, with a more prominent midrib on the underside. Leaf length and width are 0.99–(1.59)–2.35 cm and 0.26–(0.39)–0.53 cm, respectively, with a thickness of 0.16–(0.27)–0.43 mm. The male cones are catkin-like, in clusters of three on a peduncle, ranging from 5.6–(7.3)–12.0 × 1.5–(1.7)–2.1 mm, respectively. Each cone consists of entire triangular pollen scales with two round pollen sacs. Seed cones are large, ovoid drupes on a short shoot, ranging from 14.0–(20.0)–24.8 mm × 10.0–(14.0)–18.7 mm in length and width, respectively (Fig. 10).

Conservation status: IUCN: Vulnerable (VU), **Peruvian legislation:** Near Threatened (NT).

Examined specimens: PERU. Cajamarca: Prov. San Ignacio, Distr. San Ignacio, Loc. Chinchiquilla, 5°13'53"S, 78°58'26"W, 1694 m, 19-III-2018, Aguirre L. & E. Ccoica 05 (HSRI! 0545). Cajamarca: Prov. San Ignacio, Distr. Tabaconas, Loc. C.P.M. Tamborapa, 5°15'23"S, 79°06'48"W, 2094 m, 20-III-2018, E. Salazar & E. Ccoica 06 (HSRI! 0546). Pasco: Prov. Oxapampa, Distr. Villa Rica, Raimondi, Playa pampa, 10°42'50"S, 75°14'57"W, 1935 m, 09-V-2018, Aguirre L. & E. Ccoica 012 (HSRI! 00575). Pasco: Prov. Oxapampa, Distr. Oxapampa, Loc. San Francisco, 10°34'2"S, 75°24'29"W, 1819 m, 20-V-2017, E. Salazar 45 (HSRI! 0502). Pasco: Prov. Oxapampa, Distr. Chontabamba, Loc. Tunki-cueva, 10°36'22"S, 75°25'49"W, 1841 m, 19-V-2017, E. Salazar 44 (HSRI! 0501). Pasco: Prov. Oxapampa, Distr. Huancabamba, Loc. San Daniel, 10°28'54"S, 75°25'54"W, 2155 m, 24-II-2017, E. Salazar 20 (HSRI! 0478). Junín: Prov. Chanchamayo, Distr. San Ramón, Loc. nan, 11°10'59"S, 75°21'24"W, 1416 m, 27-VI-2017, E. Salazar 47 (HSRI! 0504). Junín: Prov. Chanchamayo, Distr. Chanchamayo, Loc. Monte rico-Garu, 11°02'11"S, 75°22'10"W, 1308 m, 04-V-2017, E. Salazar 38 (HSRI! 0495). Junín: Prov. Satipo, Distr. Satipo, Loc. Villa Caracol, 11°15'59"S, 74°48'10"W, 1624 m, 27-XI-2017, E. Ccoica 09 (HSRI! 0533).

DISCUSSION AND CONCLUSION

We recorded six species of Podocarpaceae in the montane forests of Peru, accounting for 50% of the total Peruvian species (Farjon, 2017; Torres Montenegro *et al.*, 2019; Khan *et al.*, 2023a). The following species were not recorded: *Pectinopitys harmsiana* (Pilg.) C. N. Page, *Podocarpus salicifolius* Klotzsch & H. Karst. ex Endl., *Podocarpus rusbyi* J. Buchholz & N. E. Gray, *Podocarpus tepuiensis* J. Buchholz & N. E. Gray, *Podocarpus parlatorei* Pilg. and *Retrophyllum piresii* (Silba) C. N. Page. However, the presence of the latter two species in Peru remains uncertain and merits further evaluation.

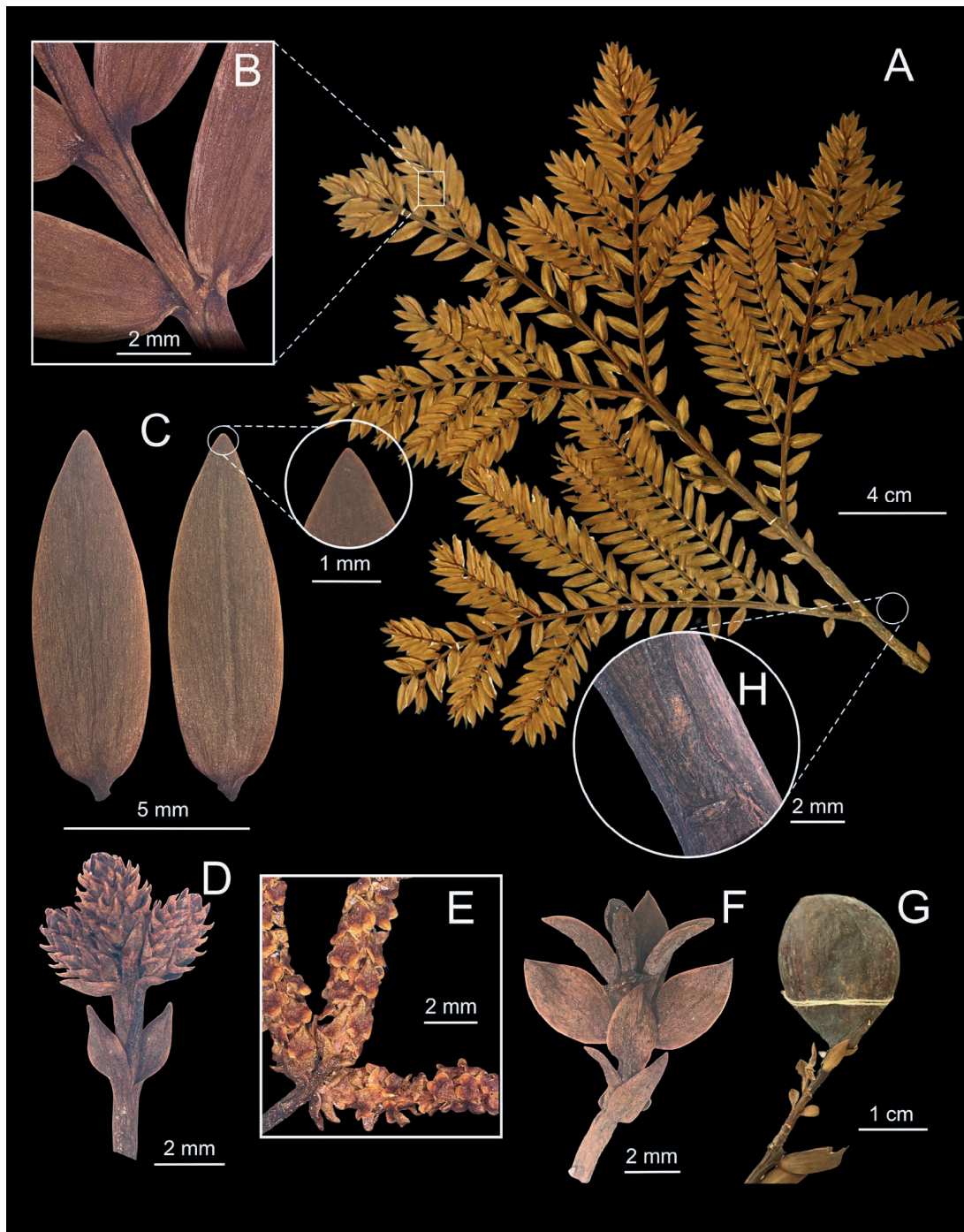


Fig. 10. *Retrophyllum rospiglosii*. A) Habit. B) Internode. C) Adaxial and abaxial leaf sides. D) Pollen cone bud. E) Pollen cone. F) Female cone. G) Seed cone. Photographs by Luis David Huayta-Hinojosa and José Antonio Ramírez Peralta. LCDP by L. D. Huayta-Hinojosa. E. Salazar 45 (HSRI!).

Fig. 10. *Retrophyllum rospiglosii*. A) Hábito. B) Entrenudo. C) Lados adaxial y abaxial de la hoja. D) Botón floral masculino. E) Cono polínico. F) Cono femenino. G) Cono semillero. Fotografías de Luis David Huayta-Hinojosa y José Antonio Ramírez Peralta. LCDP por L. D. Huayta-Hinojosa. E. Salazar 45 (HSRI!).

Regarding *R. piresii*, Mill (2016) reported its distribution as restricted to southwestern Rondônia, Brazil, near the Bolivian lowlands, and mentioned more recent but unconfirmed records from Bolivia and Peru, citing a personal communication with D. J. de Laubenfels. In the case of *P. parlatorei*, several studies indicate its distribution is limited to northern Argentina and Bolivia, without confirmed presence in Peru; nonetheless, Khan *et al.* (2023a) reported its occurrence in the Sierra de Chaglla, Huánuco Department, Peru. Given these inconsistencies, it is essential to conduct detailed taxonomic assessments of herbarium specimens and carry out fieldwork supported by fertile material and molecular data to verify the identity and distribution of these taxa within the Peruvian flora.

In Northern Peru (Cajamarca) we identified three species: *P. magnifolius*, *P. montana* and *R. rospiglosii*. Additionally, Vicuña-Miñano (2005) reported the presence of three other species: *P. harmsiana*, *P. oleifolius* and *P. sprucei*. Thus, the forests of North Peru are home to 50% of the diversity of Peruvian Podocarpaceae. In central Peru (Pasco and Junin), we recorded three species: *P. celatus*, *P. montana* and *R. rospiglosii*, which together with the presence of *P. magnifolius*, *P. oleifolius*, *P. harmsiana* reported by Marcelo-Peña & Reynel Rodríguez (2014) and Monteagudo Mendoza & Huamán Guerrero (2010) demonstrate that diversity in the central zone is comparable to that of northern Peru. In the case of southern Peru (Cusco and Apurímac), we recorded *P. glomeratus*, *P. oleifolius* and *P. montana*. Particularly, in this zone, only the presence of *P. glomeratus* was reported (Mostacero León *et al.*, 2002; Reynel *et al.*, 2006; Huamantupa-Chuquimaco *et al.*, 2017).

However, the low diversity in Southern Peru is probably due to limited biodiversity explorations and insufficient information on key taxonomic traits (for example, seed cone morphology, as highlighted by Khan *et al.* (2023b); therefore, further studies are needed to fill these information gaps.

Podocarpus celatus, *P. magnifolius* and *P. oleifolius* were categorized as Least Concern (LC) according to the IUCN Red List (IUCN, 2025), probably due to their wide distribution range. However, locally these species have a discontinuous distribution or, in many cases, are restricted to relict forests (Vicuña-Miñano, 2005; Cogollo *et al.*, 2007). Further studies are necessary to assess the degree of threat at the population level (Ames-Martínez *et al.*, 2021). On the other hand, *P. glomeratus* is considered Near Threatened (NT), while *P. montana* and *R. rospiglosii* are Vulnerable (V). The latter two species are considered to be vulnerable due to the strong anthropogenic pressure on timber resources (Antón & Reynel, 2004; Reynel *et al.*, 2006). Regarding Peruvian regulations, we verified that some species, such as *P. magnifolius* and *P. oleifolius*, which were classified as Near Threatened (NT) and Critically Endangered (CR), respectively, present a higher level of threat compared to those considered by the IUCN. By contrast, *R. rospiglosii*, changed to Near Threatened (NT).

Podocarpus glomeratus has the same category in the IUCN and in Peruvian legislation, whereas *P. celatus* as *P. montana* are not included in the list of threatened species in Peru, and therefore lack conservation status. These inconsistencies highlight the need to update and adapt the existing Peruvian regulations with the aim to include and re-evaluate the level of threat of these species at the national level. It may be also necessary to include these species in the CITES appendix.

The set of leaf morphometric descriptors analyzed in this study (length, width, area and thickness) were sufficient to group intraspecific populations, as well as to identify differences between species; therefore, they were useful traits for the taxonomic identification of the Peruvian Podocarpaceae, as found in other taxonomic studies (Buchholz & Gray, 1948a; Mill, 2015; Andruchow-Colombo *et al.*, 2024). Likewise, we recorded significant differences in leaf length, width, area and thickness among species, as described by Torres Romero (1988) in their taxonomic works on Podocarpaceae. In this regard, it has been suggested that leaf morphology is a functional trait of ecological relevance, which may have favored its radiation in the tropics (Biffin *et al.*, 2012). In tropical environments, Podocarpaceae species are neither evasive nor dominant. On the contrary, they usually occur as individual and dispersed trees surrounded by a high diversity of angiosperms, with which they even share morphological traits, such as wide and flat leaves, smooth or exfoliating bark, and seed cones that attract birds (Farjon, 2018). Recent findings by Khan & Hill (2022) suggest that these convergent features, particularly fleshy seed cones, have evolved independently across Podocarpaceae clades as adaptive responses to bird dispersal, reinforcing the functional similarity with angiosperm fruit traits. These similarities are probably due to the adaptation to tropical conditions and ecological requirements, which together generated morpho-anatomical modifications to produce greater foliar or seed cone diversity than in other conifers (Brodribb, 2011; Ornelas *et al.*, 2019).

The identification of Podocarpaceae species is essential for their conservation. In this study we demonstrate that leaf morphometric evaluation is a fast and low-cost tool for taxonomic identification. We recommend complementing these studies with cone and seed morphometry, as well as leaf anatomy, not only to improve taxonomic identification but also to better understand the evolutionary patterns of these species (Buchholz & Gray, 1948a; Andruchow-Colombo *et al.*, 2024).

Identification of Podocarpaceae species is essential for their conservation. In this study, we demonstrate that leaf morphometric analysis can be a rapid and cost-effective tool for taxonomic identification, particularly when reproductive structures are absent. We recommend that morphometric analyses be complemented with detailed studies of cone seed morphology, as well as leaf cuticle anatomy, to improve species delimitation and deepen our understanding of evolutionary patterns within the family.

The detection of inconsistencies between national and international conservation assessments underscores the importance of re-evaluating the conservation status of several species at the national level. Furthermore, our findings, based on six of the twelve Podocarpaceae species currently reported for Peru, highlight the need for an updated taxonomic synopsis of the family in the country. This should involve a comprehensive synthesis of herbarium specimens and taxonomic literature, along with targeted fieldwork in underexplored regions that may harbor undescribed species and help confirm the presence of others already reported. While our study is not exhaustive, it serves as a valuable starting point and reinforces the idea that leaf morphology can play a significant role not only in species identification but also in understanding the ecological and evolutionary dynamics of Podocarpaceae. Therefore, we recommend that future research place particular emphasis on foliar morphological traits when revising and systematizing the taxonomy of Peruvian Podocarpaceae.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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