

Rediscovery and neotypification of *Euphrasia perpusilla* (Orobanchaceae), endemic species to the Chilean Patagonian archipelagos

Author: Saldivia, Patricio

Source: *Candollea*, 79(1) : 97-105

Published By: The Conservatory and Botanical Garden of the City of Geneva (CJBG)

URL: <https://doi.org/10.15553/c2024v791a5>

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Rediscovery and neotypification of *Euphrasia perpusilla* (Orobanchaceae), endemic species to the Chilean Patagonian archipelagos

Patricio Saldivia

Abstract

SALDIVIA, P. (2024). Rediscovery and neotypification of *Euphrasia perpusilla* (Orobanchaceae), endemic species to the Chilean Patagonian archipelagos. *Candollea* 79: 97–105. In English, English and Spanish abstracts. DOI: <http://dx.doi.org/10.15553/c2024v791a5>

The rediscovery of *Euphrasia perpusilla* Phil. (Orobanchaceae), a species known only from its original description in 1858, is reported. This species, hitherto considered doubtful, is reinstated and neotypified based on specimens recently found in the Patagonian archipelagos of the Aysén Region, Chile. Its possible relationships are discussed based on morphology and distributional data. It is concluded that *E. perpusilla* is probably more directly related to taxa from Australasia than South America. Color photographs, a distribution map, and an updated key for the genus in South America are also provided.

Resumen

SALDIVIA, P. (2024). Redescubrimiento y neotipificación de *Euphrasia perpusilla* (Orobanchaceae), especie endémica de los archipiélagos de la Patagonia Chilena. *Candollea* 79: 97–105. En inglés, resúmenes en inglés y español. DOI: <http://dx.doi.org/10.15553/c2024v791a5>

Se reporta el redescubrimiento de *Euphrasia perpusilla* Phil. (Orobanchaceae), especie solamente conocida de su descripción original en 1858. Esta especie, hasta ahora considerada dudosa, se restablece y neotipifica sobre la base de especímenes recientemente descubiertos en los archipiélagos patagónicos de la región de Aysén, Chile. Se discuten sus posibles relaciones a partir de datos morfológicos y de distribución. Se concluye que probablemente *E. perpusilla* se encuentra más directamente relacionada con táxones de Australasia que de Sudamérica. Se proveen además fotografías a color, un mapa de distribución y una clave actualizada del género para Sudamérica.

Key words

OROBANCHACEAE – *Euphrasia* – Neotypification – Patagonia – South America – Taxonomy

Address of the autor:

Biota Ltda. Av. Miguel Claro 1224, Providencia, Santiago, Chile; Museo Regional de Aysén, Km 3 Camino a Coyhaique Alto, Coyhaique, Chile; O.N.G. Aumen, Coyhaique, Chile. E-mail: patricio.saldivia.perez@gmail.com

Submitted on November 11, 2023 – Accepted on March 11, 2024 – First published online on June 28, 2024
ISSN: 0373-2967 (print), 2235-3658 (online) – Published by the Conservatoire et Jardin botaniques de Genève
Open access article under Creative Commons Attribution Licence (CC BY 4.0)

Introduction

Euphrasia L. comprises some 184 species of facultative generalist, hemiparasitic, annual or perennial herbs or rarely subshrubs or shrubs (BARKER, 1982, 1986; WU et al., 2009; BROWN et al., 2021). After BARKER (1982), who estimated 161 spp., 23 new additions at the specific rank (either as new species or taxa elevated to species) have been made (IPNI, 2024). In contrast, FISHER (2004) mentioned that *Euphrasia* comprises c. 350 species but without further references, and such an estimation probably referred to the number of specific epithets that have been published since the appearance of Wettstein's monography (WETTSTEIN, 1896; see VAN ROYEN, 1983).

The genus shows mainly an antitropical distribution ranging more or less continuously across north-hemisphere temperate and holarctic areas and a fragmentary south-hemisphere temperate distribution with centers of diversity in Australia–New Zealand and the Southern Andes (BARKER, 1986). Although absent in tropical regions of central-south America, Africa, and India, *Euphrasia* shows another center of diversity in the Malasian region (sensu VAN STEENIS, 1950) and Taiwan (BARKER, 1982; WU & HUANG, 2004). However, within this tropical area, *Euphrasia* thrives only in mountainous environments (e.g. Mt. Kinabalu, see VAN STEENIS, 1964). BARKER (1982) divided the genus into 14 geographically well-delimited sections, and more recently GUSSAROVA (2005) accepted a 15th section (*vide* GUSSAROVA et al., 2008). Recent DNA-based phylogenetic analyses (e.g. GUSSAROVA et al., 2008; LI et al., 2019) have shown that *Euphrasia* is monophyletic. However, MORTIMER et al. (2022) found *Euphrasia* paraphyletic, as the monotypic *Omphalotrix* Maxim. was nested within it. At the sectional level, sampling in those studies has been insufficient to test the monophyly of most of them, especially in the southern hemisphere. A recent phylogenomic study (GARRET et al., 2022) showed that phylogenetic discordance in *Euphrasia* is extensive at both deeper and shallower nodes.

Following the recent taxonomic revision of *Euphrasia* in South America by ORTIZ et al. (2021), plus the description of a new species by SANTOS et al. (2021), the genus is integrated by nine species in the region. Seven of these species are grouped in sect. *Trifidae* Benth. (BARKER, 1982). This section ranges from Tierra del Fuego and Islas Malvinas in the southern tip of the continent to the north across the Andes, reaching the Atacama Region in Chile, Jujuy in Argentina, and Potosí in Bolivia. The other two are *E. formosissima* Skottsb. (sect. *Paradoxae* Pugsley), endemic to the Juan Fernández Archipelago, and *E. officinalis* L. (sect. *Euphrasia*), an adventive species from Eurasia.

In the recent revision by ORTIZ et al. (2021), the authors considered three doubtful taxa, two from Peru (*Euphrasia pubescens* Benth. and *E. tripartita* Ruiz & Pav.) and one from Chile, *E. perpusilla* Phil., described in 1858 by Rudolph A. Philippi (1808–1904). Since its description, this species

was not collected again until now, and the type material has not been found (MUÑOZ-PIZARRO, 1960; ORTIZ et al., 2021). In the present work, I reinstate this species by providing a comprehensive morphological description and ecological data. The name is also neotypified.

Materials and methods

Plants of *Euphrasia perpusilla* were found in January 2023 in the Katalalixar National Reserve (Fig. 1). Individuals were photographed in situ using an Olympus Tough TG-6 digital camera (Tokyo, Japan), and ecological and vegetational data were compiled. Collections were deposited at MURAY and SGO.

Morphological characters were analyzed following specialized taxonomic literature (e.g. ASHWIN, 1961; BARKER, 1982; VAN ROYEN, 1983; ORTIZ et al., 2021), using a light stereomicroscope Euromex Nexius Zoom EVO (Arnhem, The Netherlands), after structures had been rehydrated in boiling water for 1–2 minutes.

Taxonomy

Euphrasia perpusilla Phil. in *Linnaea* 29: 28. 1858 (Fig. 2, 3).

Neotypus (designated here): **CHILE. Reg. de Aysén:** Prov. de Capitán Prat, Reserva Nacional Katalalixar, Isla Campana, Angostura Chilena, creciendo en turbera de *Donatia–Astelia*, [48°34'01"S 75°13'46"W], 31 m, 9.I.2023, *Saldivia & Faúndez 4211* (MURAY [MURAY-BV02090]!; isoneo-: SGO!). Holotypus: **CHILE. Reg. de Aysén:** insulis Chonos [Chonos Archipelago], c. 245 m, s.d., *Fonk* (not located).

Annual herbs, 17–22 mm tall. *Stems* purplish, glabrous, or with sparse eglandular trichomes, erect, unbranched, with 2–3 nodes with well-developed leaves and 2 with underdeveloped leaves towards the apex. *Cotyledons* 2 mm long, green, oblong, entire, persistent. *Leaves* opposite, sessile, obovate, base truncate to slightly cuneate, succulent, 3–5-lobed; upper lobes with margin bluntly broad-obtuse, thickened and cucullate, papillose in the abaxial surface (visible only after dissection when cucullate area is unfolded) and scaberulous in the adaxial surface, lobes green, blade upper portion green and purplish towards the nodes; leaves from the first node 3 × 1.8 mm, 3-nerved, one apical lobe and two diminutive lateral ones (one in each side of the blade); leaves of the second node 4 × 2.5 mm, with lateral lobes more developed, 5-nerved; the leaves from the third node reach the largest size, 4.2 × 2.8 mm, 5-lobed, one apical and two lateral on each side of the blade decreasing in size towards the base; bracts like the leaves from the second node but narrower. *Flowers* axillary, sessile, acropetally, and decussately developed in the

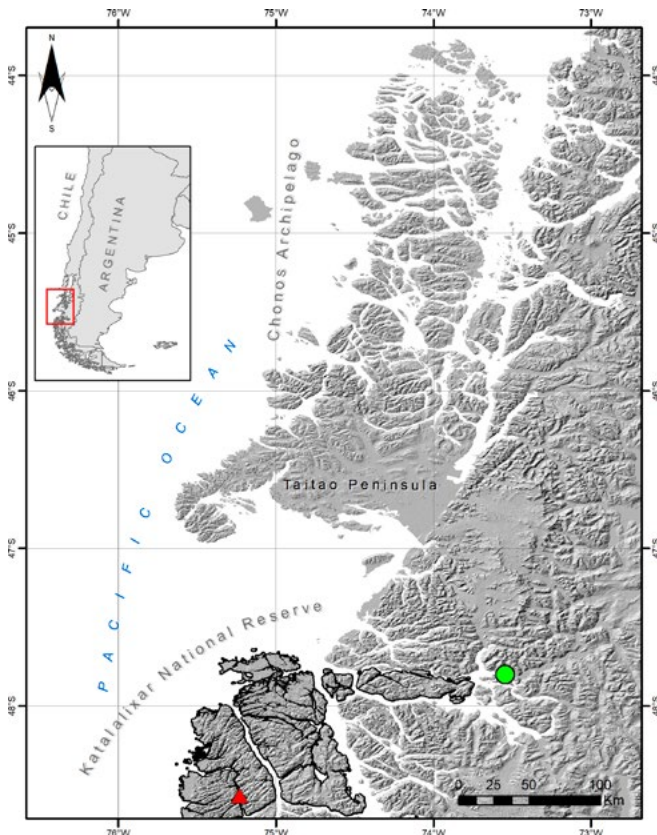


Fig. 1. – Map of the Patagonian archipelagos of the Aysén Region showing the Chonos Archipelago, Katalalixar National Reserve (black outline), and the new locality (red triangle). The nearest town, Caleta Tortel, is represented by a green dot.

second and third nodes; above that, only small undeveloped buds in the axils of the apical congested underdeveloped leaves. *Calyx* 3.5 × 1.5 mm (3.5–4 mm when dissected), green and purplish towards the margins, glabrous, 4-lobed; lobes 1–1.5 mm long, apex rounded and thickened. *Corolla* hooded, 2-lipped, upper lip 2-lobed, lower lip 3-lobed, ground color white with 3 violet nectar guides per lobe running from the middle part of the tube to near the lobe apices, mostly glabrous except for the outer surface of the hood, which is covered by eglandular short trichomes not extending to the lobes or tube; corolla upper side 5–5.2 mm long, tube 3.5 mm long with the anterior filaments attached at 1.7 mm from corolla base, hood 1.2 × 1 mm (excluding lobes), upper lip 1.5 × 1.5 mm, cleft between upper lobes 0.3 mm depth, lower lip 1.5 × 3 mm, cleft between lower lobes 0.5 mm depth, lobes slightly emarginate to rounded. *Androecium* didynamous, anthers 0.8 × 0.3 mm, free, clustered and enclosed below the hood, awns 0.2 mm long, slits glabrous. *Ovary* 1.5 × 1.2 mm, oblong, glabrous; style c. 3 mm long, curved downwards below the hood, quick withered after anthesis; stigma 0.3 mm long, short papillose. *Capsules* 2.5 × 1.5 mm (immature), oblong-elliptic, glabrous, dark brown, lustrous. *Seeds* c. 7, 1 × 0.5 mm, ellipsoid.

Distribution. – Endemic to the Chilean Patagonian archipelagos of the Aysén Region. Apart from the *locus classicus*, the species is known only from the presently recorded locality (Fig. 1). Based on the recent revision of ORTIZ et al. (2021), *Euphrasia perpusilla* is the only species of the genus distributed in the archipelagos of western Patagonia.

Habitat. – Individuals of *Euphrasia perpusilla* were found growing on hygrophilous, mostly ombrotrophic, and poorly-drained pulvinate herbaceous communities dominated by *Donatia fascicularis* J.R. Forst. & G. Forst., *Astelia pumila* (G. Forst.) Gaudich., and *Schoenus antarcticus* (Hook. f.) Dusén, which are commonly surrounded by the dwarf podocarp *Lepidothamnus fonkii* Phil. Most of the flora associated with this vegetation are diminutive herbs such as *Caltha appendiculata* Pers., *C. dioneifolia* Hook. f., *Drosera uniflora* Willd., *Gaimardia australis* Gaudich., *Gentianella* sp., *Oreobolus obtusangulus* Gaudich., *Microschizaea fistulosa* (Labill.) C.F. Reed, *Tapeinia pumila* (G. Forst.) Baill., and some small repent or procumbent shrubs like *Gaultheria antarctica* Hook. f., *G. pumila* (L. f.) D.J. Middleton, and *Myrteola nummularia* (Poir.) O. Berg. (see Fig. 2A, B). This community occurs patchily among areas of exposed old intrusive rocks (granitoid) deposited mostly during the Early Cretaceous in what is known as the South Patagonian Batholith (SERNAGEOMIN, 2002; HERVÉ et al., 2007), thickets of *Metrosideros stipularis* (Hook. & Arn.) Hook. f. (= *Tepualia stipularis* (Hook. & Arn.) Griseb.), and patches of stunted forests of *Pilgerodendron uviferum* (D. Don) Florin, *Nothofagus antarctica* (G. Forst.) Oerst., *N. betuloides* (Mirb.) Oerst., and *Podocarpus nubigenus* Lindl.

This community, widely distributed in archipelagos and coastal mainland areas with oceanic influence in western Patagonia, conforms the Magellanic Moorland (GODLEY, 1960) or Tundra Complex (PISANO, 1983), which ranges chiefly from Tres Montes Peninsula and the Gulf of Penas area (Fig. 1) southwards to the end of the Patagonian archipelagos (c. 56°S). North of Tres Montes Peninsula, this community becomes patchy and less common, reaching as north as 38°S in the Nahuelbuta Coastal Range (VILLAGRÁN, 1988, 2001; RAMÍREZ et al., 2023).

Conservation status. – After its description in 1858, *Euphrasia perpusilla* was not recorded again until now. Nevertheless, the distance between the *locus classicus* and the new locality suggests that *E. perpusilla* may be distributed across the whole archipelagic area of the Aysén Region (Fig. 1), and probably in the northern part of the Magallanes Region. Western Patagonia in the Aysén Region has been proposed as a transition area between Valdivian and Magellanean provinces (RIVAS-MARTÍNEZ et al., 2011), as well as between the North-Patagonian and Magellanean forests (ARROYO et al., 1997).



Fig. 2. – *Euphrasia perpusilla* Phil. **A, B.** Plants among associate flora and vegetation (Df: *Donatia fascicularis*, Lf: *Lepidothamnus fonkii*, Oo: *Oreobolus obtusangulus*, Du: *Drosera uniflora*, Ga: *Gaultheria antarctica*); **C, D.** Frontal view of the flowers; **E, F.** Lateral view of the flowers. [Saldivia & Faúndez 4211] [Photos: P. Saldivia]



Fig. 3. – *Euphrasia perpusilla* Phil. A. Leaf of the third node; B. Leaf of the first node; C. Dissected calyx; D. Anthers; E. Immature capsule; F. Calyx. [Saldivia & Faúndez 4211] [Photos: P. Saldivia]

However, all the archipelagic area of Aysén is classified under the same macrobioclimate, ombrotype, termotype, continentality, and bioclimate (LUEBERT & PLISCOFF, 2017). Therefore, instead of considering *E. perpusilla* as an extremely rare or scarce species, its lack of collections is most likely due to its small size (barely emerging from *Donatia* cushions), annual life cycle, and the difficult access of the region where it grows. Accordingly, the category Data Deficient (DD) is assigned because data are inadequate to determine a threat category (IUCN, 2012).

Notes. – *Euphrasia perpusilla* was described based on material from: “*In insulis Chonos circa 800 pedes supra mare legit orn. Dr. Fr. Fonk*” (PHILIPPI, 1858). Francisco Fonck (1830–1912) was a German doctor and naturalist who arrived in Chile in 1854 and visited the Chonos archipelago in 1857 as part of a hydrographic expedition (PHILIPPI, 1914). He was an avid plant collector and collaborator of R.A. Philippi, who published 69 new species based on Fonck’s collections (MACAYA & FONCK, 2005). Philippi’s types from Chilean taxa are in SGO (STAFLEU & COWAN, 1983), however, the material concerning *E. perpusilla* is missing. In this line, MUÑOZ-PIZARRO (1960) and MUÑOZ-SCHICK (1973) did not provide any information either about the original material. ORTIZ et al. (2021) also reported that they were unable to locate the type. A recent consultation with the SGO staff confirmed that there is no original material of the species in SGO (J. Arriagada, pers. comm.). On this basis, the name *E. perpusilla* is here neotypified.

The morphological description by PHILIPPI (1858) in the protologue, although brief, provides key features allowing the identification of the new collection as *Euphrasia perpusilla*. The few vegetative and floral measurements given in the protologue are almost identical to those obtained from the recently collected specimens. Moreover, the apically rounded lobes of the calyx (“*laciniis calycinis linearibus, apice rotundatis*”) is one of the characters that unequivocally separates *E. perpusilla* from the remaining South American species, which have lobes with acute apex (ORTIZ et al., 2021).

According to BARKER (1982), *Euphrasia perpusilla* belongs to sect. *Trifidae*. However, this classification may be uncertain since it could have only been based on the brief original description and location. *Euphrasia perpusilla* is morphologically puzzling and so, its taxonomic position is unclear and it should be treated as *incertae sedis* until phylogenetic evidence is analyzed with sufficient and robust sampling. *Euphrasia perpusilla* has free and glabrous anthers, which are features only shared with mainland South American species (sect. *Trifidae*) and *E. disperma* Hook. f. from New Zealand (BARKER, 1982). However, several characters suggest a closer relationship with other Australasian groups.

The hood of the corolla’s upper lip is lacking in sect. *Trifidae* (ORTIZ et al., 2021), however, is a conspicuous feature of *Euphrasia perpusilla* as in most of the New Guinean species

(VAN ROYEN, 1972, 1983), and many others from New Zealand and Australia (BARKER, 1982). The stigma in sect. *Trifidae* is obscurely bilobed with the upper lobe reduced, appearing almost capitate (ORTIZ et al., 2021). In *E. perpusilla* the stigma morphology conforms to what VAN ROYEN (1983) described for the species from New Guinea: “stigma obliquely and unequally 2-lipped”, such as he illustrated for *E. scutellarioides* Wernham and *E. callosa* Pennell. In sect. *Trifidae*, the leaves are trilobed (only in *E. adenonota* I.M. Johnst.), trisected, or triparted (ORTIZ et al., 2021), with deep incisions separating the leaf divisions which are more or less of similar size, leaving a reduced blade area (i.e. the part of leaf or bract excluding the teeth and, if present, the attenuate part of the base, sensu BARKER, 1982). In contrast, *Euphrasia perpusilla* has leaves varying from 3 to 5-lobed, with the basal lobes inconspicuous or significantly smaller than the others, and shallow incisions, leaving a large blade area (Fig. 3A, B). In *E. perpusilla*, like most of the New Guinea species, the lobes are unequal in size, with an apical median rounded lobe considerably wider than the lateral ones, which decreases in size towards the leaf base. Additionally, in *E. perpusilla* the lobes are cucullate (Fig. 3A, B), a morphological feature only known from most of the New Guinean species (VAN ROYEN, 1972, 1983), which BARKER (1982) described as “oddly hooded”. The leaves of *E. adenonota* seem also to be slightly cucullate (see fig. 4B in ORTIZ et al., 2021), but several other morphological features, like its almost actinomorphic corolla, point to rule out a closer relationship between it and *E. perpusilla*.

From a phytogeographic point of view, similar cushion bog communities to the ones where *Euphrasia perpusilla* thrives are those dominated by *Donatia novae-zelandiae* Hook. f. from New Zealand and Tasmania (COCKAYNE, 1921; KIRKPATRICK, 1977, 1997; GIBSON & KIRKPATRICK, 1985). Additionally, phylogenetic relationships of species integrating the communities associated with *E. perpusilla* show a pattern of transpacific affinities with Australasia (e.g. *Astelia* [BIRCH et al., 2012], *Donatia* J.R. Forst. & G. Forst. [WAGSTAFF & WEGE, 2002; CAROLIN, 2007], *Drosera* L. [RIVADAVIA et al., 2003], *Gaimardia* Gaudich. [COOKE, 1998; FORD, 2014], *Lepidothamnus* Phil. [KLAUS & MATZKE, 2020], *Metrosideros* Banks ex Gaertn. [PILLON et al., 2015], and the *Phyllachne* J.R. Forst. – *Forstera* L. f. complex [WAGSTAFF & WEGE, 2002; CAROLIN, 2007]). Some authors have proposed that early Gondwanian connections explain such a pattern (DU RIETZ, 1960; BARKER, 1982, 1986; HEADS, 2014).

Finally, considering the conservative taxonomic approach proposed by ORTIZ et al. (2021), and adding *Euphrasia achibuenoensis* and *E. perpusilla*, *Euphrasia* in South America includes nine endemic species plus one adventitious from Eurasia (see updated key below). Based on morphological and phytogeographic evidence, the closest relationships of

E. perpusilla seem to lie towards Australasia rather than mainland South America.

Key to the species of *Euphrasia* in South America

[modified from ORTIZ et al., 2021]

1. Leaves 4–10-toothed or crenated; anthers fused 2
- 1a. Leaves 3–5-lobed, 3-sected, or 3-parted; anthers free 3
2. Small shrubs; calyx with 4 equal triangular teeth with obtuse apex or deltoid teeth with rounded apex; endemic to Juan Fernández Islands *E. formosissima*
- 2a. Herbs; calyx with 4 unequal triangular teeth with narrowly acute sharp apex; European, adventive, not present in Juan Fernández Islands *E. officinalis*
3. Leaves 3–5-lobed with obtuse apex; corolla tube 2.5–4.5 mm long 4
- 3a. Leaves 3-partite or 3-sected with acute apex; corolla tube 5–30 mm long 5
4. Lobes equal to subequal in size; corolla upper lip not hooded *E. adenota*
- 4a. Lobes unequal in size, with apical median lobe considerably wider than lateral ones; corolla upper lip hooded *E. perpusilla*
5. Leaves pubescent on both surfaces *E. antarctica*
- 5a. Leaves glabrous or occasionally sparsely puberulent 6
6. Corolla obscurely 2-lipped, appearing tubular, yellow, orange, red, or rarely white 7
- 6a. Corolla noticeably 2-lipped, lower lip white with yellow blotch or rarely completely yellow, generally with violet nectar guides 8
7. Corolla yellow or rarely white *E. andicola*
- 7a. Corolla red, orange, or both *E. achibuenoensis*
8. Stem oppositely branched above ground level in successive nodes *E. trifida*
- 8a. Stem ramification restricted to ground level 9
9. Basal internodes short with leaves densely disposed and overlapping, apical internodes longer with leaves not overlapping *E. muscosa*
- 9a. Basal and apical internodes equal in length, leaves never densely disposed or overlapping *E. subexserta*

Acknowledgements

The discovery of *Euphrasia perpusilla* was made during fieldwork through the Patagonian archipelagos of the Aysén Region as part of the project “Monitoring changes and updating the cadaster of native vegetation in the Aysén Region of General Carlos Ibáñez del Campo” developed by Biota Ltda.

for the Chilean Forestry Corporation (CONAF). Much appreciation to the CONAF, and particularly, to Françoise Pincheira and Víctor Lagos San Marín for their assistance in getting the Authorization (N° 32/2023) to carry out research activities at the Chilean National System of State Protected Areas (SNASPE). I also thank Jimena Arriagada for her assistance regarding R.A. Philippi’s types at SGO and to the Regional Museum of Aysén’s staff for facilitating their dependencies for lab work. Much gratitude to Duncan Nicol for sending literature and reviewing an early draft of this study, to Matías Treumun for the elaboration of Figure 1, and to Leonardo Pérez for geological input. Special thanks to Joel Calvo and one anonymous reviewer for their comments and suggestions that helped to substantially improve this contribution. Sailing was on board the “Paz Austral” under the command of Captain Noel Vidal and María Paz Hargreaves. I am immensely grateful to Noel, María Paz, Alejandro Moreno (cook), and my colleagues Luis Faúndez, Matías Treumun, and Leonardo Pérez for their help and excellent company in the field.

References

- ARROYO, M.T.K., L.A. CAVIERES, A. PEÑALOZA, M. RIVEROS & A.M. FAGGI (1997). Relaciones fitogeográficas y patrones regionales de riqueza de especies en la flora del bosque lluvioso templado de Sud América. In: ARMESTO, J.J. et al. (ed.), *Ecología de los Bosques Nativos de Chile*: 71–99. Editorial Universitaria, Santiago.
- ASHWIN, M.B. (1961). *Euphrasia*. In: ALLAN, H.H. (ed.), *Flora of New Zealand: Volume I, Indigenous Tracheophyta, Psilopsida, Lycopsida, Filicopsida, Gymnospermae, Dictyledones*: 849–860. Government Printer, Wellington.
- BARKER, W.R. (1982). Taxonomic studies in *Euphrasia* L. (Scrophulariaceae). A revised infrageneric classification and a revision of the genus in Australia. *J. Adelaide Bot. Gard.* 5: 1–304.
- BARKER, W.R. (1986). Biogeography and evolution in *Euphrasia* (Scrophulariaceae), particularly relating to Australia. In: Barlow, B.A. (ed.), *Flora and fauna of alpine Australia, ages and origins*: 489–510. CSIRO, Melbourne.
- BIRCH, J.L., S.C. KEELEY & C.W. MORDEN (2012). Molecular phylogeny and dating of Asteliaceae (Asparagales): *Astelia* s.l. evolution provides insight into the Oligocene history of New Zealand. *Molec. Phylog. Evol.* 65: 102–115.
- BROWN, M.R., P.G.P. MOORE & A.D. TWYFORD (2021). Performance of generalist hemiparasitic *Euphrasia* across a phylogenetically diverse host spectrum. *New Phytol.* 232: 2165–2174.
- CAROLIN, R.C. (2007). Styliaceae. In: KADEREIT, J.W. & C. JEFFREY (ed.), *Families and Genera of Vascular Plants. Flowering Plants, Eudicots, Asterales*, vol. 8: 614–619. Springer-Verlag, Berlin.
- COCKAYNE, L. (1921). *The Vegetation of New Zealand, Ed. 1, Die Vegetation der Erde, XIV*. Wilhelm Engelmann, Leipzig.

- COOKE, D.A. (1998). Centrolepidaceae. In: KUBITZKI, K. (ed.), *The Families and Genera of Vascular Plants. Flowering Plants, Monocotyledons, Alismatanae and Commelinanae (except Gramineae)*, vol. 4: 106–109. Springer-Verlag, Berlin.
- DU RIETZ, G.E. (1960). Remarks on the botany of the southern cold temperate zone. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 152: 500–507.
- FISHER, E. (2004). Scrophulariaceae. In: KUBITZKI, K. (ed.), *The Families and Genera of Vascular Plants. Flowering Plants, Dicotyledons, Lamiales (except Acanthaceae including Avicenniaceae)*, vol. 7: 333–432. Springer-Verlag, Berlin.
- FORD, K.A. (2014). Centrolepidaceae. In: BREITWIESER, I. et al. (ed.), *Flora of New Zealand – Seed Plants*, fasc. 2: 1–24. Manaaki Whenua Press, Lincoln.
- GARRETT, P., H. BECHER, G. GUSSAROVA, C.W. DEPAMPHILIS, R.W. NESS, S. GOPALAKRISHNAN & A.D. TWYFORD (2022). Pervasive Phylogenomic Incongruence Underlies Evolutionary Relationships in Eyebrights (*Euphrasia*, Orobanchaceae). *Frontiers Pl. Sci.* 13: 869583. DOI: <https://doi.org/10.3389/fpls.2022.869583>
- GIBSON, N. & J.B. KIRKPATRICK (1985). A comparison of the cushion plant communities of New Zealand and Tasmania. *New Zealand J. Bot.* 23: 549–566.
- GODLEY, E.J. (1960). The botany of southern Chile in relation to New Zealand and the Subantarctic. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 152: 457–475.
- GUSSAROVA, G. (2005). Synopsis of the genus *Euphrasia* L. (Scrophulariaceae) of Russia and adjacent states (within the limits of the former USSR). *Bot. Zhurn. (Moscow, Leningrad)* 90: 1087–1115.
- GUSSAROVA, G., M. POPP, E. VITEK & C. BROCHMANN (2008). Molecular phylogeny and biogeography of the bipolar *Euphrasia* (Orobanchaceae): Recent radiations in an old genus. *Molec. Phylogen. Evol.* 48: 444–460.
- HEADS, M. (2014). *Biogeography of Australasia: A molecular analysis*. Cambridge University Press, Cambridge, UK.
- HERVÉ, F., R.J. PANKHURST, C.M. FANNING, M. CALDERÓN & G.M. YAXLEY (2007). The South Patagonian batholith: 150 my of granite magmatism on a plate margin. *Lithos* 97: 373–394.
- IPNI (2024). *International Plant Names Index*. Royal Botanic Gardens, Kew, Harvard University Herbaria & Libraries and Australian National Herbarium. [<http://www.ipni.org>]
- IUCN (2012). *IUCN Red List Categories and Criteria*. Version 3.1. Ed. 2. IUCN Species Survival Commission, IUCN Gland & Cambridge.
- KIRKPATRICK, J.B. (1977). Vegetation of the west coast region. In: BANKS, M.R. & J.B. KIRKPATRICK (ed.), *Landscape and man*: 55–80. Royal Society of Tasmania, Hobart.
- KIRKPATRICK, J.B. (1997). *Alpine Tasmania: an illustrated guide to the flora and vegetation*. Oxford University Press, Melbourne.
- KLAUS, V.K. & N.J. MATZKE (2020). Statistical comparison of trait-dependent biogeographical models indicates that Podocarpaceae dispersal is influenced by both seed cone traits and geographical distance. *Syst. Biol.* 69: 61–75.
- LI, X., T. FENG, C. RANDLE & G.M. SCHNEEWEISS (2019). Phylogenetic relationships in Orobanchaceae inferred from low-copy nuclear genes: consolidation of major clades and identification of a novel position of the non-photosynthetic Orobanche clade sister to all other parasitic Orobanchaceae. *Frontiers Pl. Sci.* 10: 902.
- LUEBERT, F. & P. PLISCOFF (2017). *Sinopsis bioclimática y vegetal de Chile*. Ed. 2. Editorial Universitaria, Santiago.
- MACAYA, J.H. & A. FONCK (2005). Francisco Adolfo Fonck Foveaux (1830–1912) y su importancia en la botánica chilena del siglo XIX y XX. *Chloris Chilensis* 8(2): 35–44. [<http://www.chlorischile.cl>]
- MORTIMER, S.M.E., J. BOYKO, J.M. BEAULIEU & D.C. TANK (2022). Synthesizing existing phylogenetic data to advance phylogenetic research in Orobanchaceae. *Syst. Bot.* 47: 533–544.
- MUÑOZ-PIZARRO, C. (1960). *Las especies de plantas descritas por R. A. Philippi en el siglo XIX*. Ediciones de la Universidad de Chile, Santiago.
- MUÑOZ-SCHICK, M. (1973). Complemento de “Las especies de plantas descritas por R. A. Philippi en el siglo XIX.” *Anales Univ. Chile*, ser. 3, 128: 5–69.
- ORTIZ, A.V., P. MORONI, F. MIRRA, M.R. VILLANUEVA & N. O’LEARY (2021). Taxonomic revision of *Euphrasia* (Orobanchaceae) in South America. *Ann. Missouri Bot. Gard.* 106: 392–423.
- PHILIPPI, R.A. (1858). *Plantarum novarum chilensium*. *Linnaea* 29: 1–110.
- PHILIPPI, F. (1914). Historia del Museo Nacional de Chile por el Dr. R. A. Philippi. *Bol. Mus. Nac. Chile* 7: 13–47.
- PILLON, Y., E. LUCAS, J.B. JOHANSEN, T. SAKISHIMA, B. HALL, S.M. GEIB & E.A. STACY (2015). An expanded *Metrosideros* (Myrtaceae) to include *Carpolepis* and *Tepualia* based on nuclear genes. *Syst. Bot.* 40: 782–790.
- PISANO, E. (1983). Magellanic Tundra complex. In: GORE, A.J.P. (ed.), *Ecosystems of the World: Mires, Swamps, Bogs, Fen and Moor, B. Regional Studies*: 295–329. Elsevier, Amsterdam.
- RAMÍREZ, C., J. VALENZUELA, O. VIDAL, J.M. FARIÑA, C. SAN MARTÍN, A. MARTICORENA & O. VALDIVIA (2023). Humedales turbosos del Parque Nacional Nahuelbuta (Región de la Araucanía) comparados con otros, en un gradiente latitudinal de Chile. *Gayana, Bot.* 80: 16–37.
- RIVADAVIA, F., K. KONDO, M. KATO & M. HASEBE (2003). Phylogeny of the sundews, *Drosera* (Droseraceae), based on chloroplast *rbcl* and nuclear *18S* ribosomal DNA sequences. *Amer. J. Bot.* 90: 123–130.

- RIVAS-MARTÍNEZ, S., G. NAVARRO, A. PENAS & M. COSTA (2011). Biogeographic map of South America. A preliminary survey. *Int. J. Geobot. Res.* 1: 21–40.
- ROYEN, P. VAN (1972). The Scrophulariaceae of the alpine regions of New Guinea. *Bot. Jahrb. Syst.* 91: 383–437.
- ROYEN, P. VAN (1983). *Euphrasia*. In: Royen, P. van (ed.), *The Alpine Flora of New Guinea. Taxonomic part: Casuarinaceae to Asteraceae*, vol. 4: 2897–2921. Cramer, Vaduz.
- SANTOS, D., J.M. WATSON & R.A. FLORES (2021). A new species of *Euphrasia* L. (Orobanchaceae) endemic to Maule Region in central-southern Chile. *Rock Gard.* 144: 13–53.
- SERNAGEOMIN (2002) *Mapa Geológico de Chile. Carta Geológica de Chile*. Serie Geología Básica. Servicio Nacional de Geología y Minería. No. 75. Escala 1:1.000.000.
- STAFLEU, F.A. & R.S. COWAN (1983). Taxonomic literature, vol. 4. *Regnum Veg.* 110.
- STEENIS, C.G.G.J. VAN (1950). The delimitation of Malaysia and its main plant geographical divisions. *Fl. Malesiana, Ser. I*, 1: 1xx–1xxv.
- STEENIS, C.G.G.J. VAN (1964). Plant geography of the mountain flora of Mt Kinabalu. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 161: 7–38.
- VILLAGRÁN, C. (1988). Expansion of Magellanic Moorland during the Late Pleistocene: palynological evidence from northern Isla de Chiloé, Chile. *Quatern. Res.* 30: 304–314.
- VILLAGRÁN, C. (2001). Un modelo de la historia de la vegetación de la Cordillera de la Costa de Chile central-sur: La hipótesis glacial de Darwin. *Revista Chilena Hist. Nat.* 74: 793–803.
- WAGSTAFF, S.J. & J. WEGE (2002). Patterns of diversification in New Zealand Stylidiaceae. *Amer. J. Bot.* 89: 865–874.
- WETTSTEIN, R. VON (1896). Monographie der Gattung *Euphrasia*. *Arbeiten Bot. Inst. K. K. Deutsch. Univ. Prag.* 9.
- WU, M.-J. & T.-C. HUANG (2004). Taxonomy of the *Euphrasia transmorrisonensis* (Orobanchaceae) complex in Taiwan based on nrITS. *Taxon* 53: 911–918.
- WU, M.-J., T.-C. HUANG & S.-F. HUANG (2009). Phylogenetic biogeography of *Euphrasia* section *Malesianae* (Orobanchaceae) in Taiwan and Malesia. *Blumea* 54: 242–247.