GAYANA BOTANICA
Gayana Bot. (2025) vol. 82, No. 1, 121-127

SHORT COMMUNICATION

Potential pollinators and capsule formation in four *Chloraea* (Orchidaceae) species from south-central Chile

Polinizadores naturales y formación de cápsulas en cuatro especies de *Chloraea* (Orchidaceae) del centro-sur de Chile

Guillermo Pereira[1], Christian Troncoso[1], Diyanira Castillo-Novales[2,3], Orlando Jeldes-Cajas[4], Joel Tupac Otero[5], César Arriagada[6] & Cristian Atala[4,*]

[1]Laboratorio Biotecnología de Hogos, Departamento de Ciencias y Tecnología Vegetal, Universidad de Concepción, Campus Los Ángeles, Casilla 234, Los Ángeles, Chile.
[2]Laboratorio de Microbiología Molecular y Biotecnología Ambiental, Departamento de Química, Universidad Técnica Federico Santa María, Avenida España 1680, Valparaíso 2390123, Chile.
[3]Escuela de Agronomía, Facultad de Ciencias Agronómicas y de los Alimentos, Pontificia Universidad Católica de Valparaíso, San Francisco s/n La Palma, Quillota 2260000, Chile.
[4]Instituto de Biología, Facultad de Ciencias, Pontificia Universidad Católica de Valparaíso, Campus Curauma, Avenida Universidad 330, Valparaíso, Chile.
[5]Departamento de Ciencias Básicas, Sede Palmira, Universidad Nacional de Colombia, Carrera 32 # 12-00 Palmira, Valle del Cauca, Colombia.
[6]Departamento de Ciencias Forestales, Facultad de Ciencias Agropecuarias y Medioambiente, Universidad de la Frontera, Casilla 54-D, Temuco, Chile.
*Corresponding author: cristian.atala@pucv.cl

ABSTRACT

We studied the potential pollinators of four *Chloraea* orchid species that grow sympatrically in Central-South Chile. We recorded potential pollinator visits, and evaluated capsule formation after 30 days. Results revealed Coleoptera and Hymenoptera species as potential pollinators, with no specific preference for any orchid species. Many visited flowers aborted, leading to low capsule formation, especially in *C. lamellata*. These findings enhance our understanding of Chilean orchid biology, aiding in their conservation efforts.

Keywords: natural pollination, orchid pollinators, terrestrial orchids.

RESUMEN

Estudiamos los polinizadores de cuatro especies de orquídeas del género *Chloraea* que crecen simpátricamente en el centro-sur de Chile. Registramos visitas de probables polinizadores y evaluamos la formación de cápsulas treinta días después mediante observaciones de campo. Encontramos Coleoptera e Hymenoptera como polinizadores, sin preferencia por especies de orquídeas. Muchas flores visitadas abortaron, lo que provocó baja formación de cápsulas, especialmente en *C. lamellata*. Estos resultados aportan al conocimiento de la biología de las orquídeas chilenas y favorecen su conservación.

Palabras clave: orquídeas terrestres, polinización natural, polinizadores de orquídeas.

INTRODUCTION

Orchidaceae is one of the largest and most diverse families of flowering plants, comprising over 25,000 species (Dressler 1993; Heywood *et al.* 2007; Reina-Rodríguez *et al.* 2010). Orchid species constitute an advanced and taxonomically intricate group, highly specialized and with complex biological interactions (Rasmussen 2002), including one of the most awesome and intriguing examples of complex interactions with pollinators (Roberts 2003; Scopece *et al.* 2015). The orchid-pollinator interaction seems to be so ancient that the fossil of the extinct orchid *Meliorchis caribea* was found together with the stingless bee *Proplebeia dominicana* (Hymenoptera: Apidae), with the respective pollinium attached to its body (see Ramírez *et al.* 2007). Orchid pollination is extremely diversified, including rewarding and deceptive systems and

Open Access Journal
©2025 The Author(s). This open access article is distributed under the terms of the Creative Commons Attribution-NonCommercial 4.0 International License (CC BY-NC 4.0), which permits any noncommercial use, distribution, and reproduction, as long as appropriate credit is given to the original author(s) and the source.

various behavior types (Dressler 1993). This variation in motivation and outcome of flower visits by the pollinator is expected to affect patterns of pollinator specialization (Schiestl & Schluter 2009). Close to a 97 % of all orchid species require a pollinator (mostly insects), with about 60 % interacting with a single pollinator species (Tremblay 1992), suggesting an important adaptive process in the family (Cozzolino & Widmer 2005).

The morphological diversity of orchid flowers reflects several adaptations to a wide range of pollinators (Johnson & Steiner 2000; Herrera *et al.* 2006; Kaur 2019), usually attracting pollinators via visual and/or chemical clues (Tremblay *et al.* 2005; Micheneau *et al.* 2009; Duque-Buitrago *et al.* 2014). Pollinators are usually insects including bees and wasps (order Hymenoptera), though species from the Lepidoptera, Diptera, Coleoptera, and others also pollinate orchids, as do some small birds (Statman-Weil 2001; Hawkeswood & Turner 2004; Lehnebach & Robertson 2004; Micheneau *et al.* 2010; Newman *et al.* 2011; Stökl *et al.* 2011). A few previous studies in Chile have reported the presence of species of the orders Hymenoptera and Diptera as probable pollinators as they were observed carrying pollinia attached to the torax, also some species of the orders Lepidoptera and Coleoptera have been described, but only as visitors (Lehnebach & Riveros 2003; Humaña *et al.* 2008; Cuartas-Domínguez & Medel 2010; Monzón *et al.* 2019). However, for most species the identity, attraction strategy, dependency, and success of pollination is unknown. Existing data show that Chilean orchids, *Chloraea* species in particular, the most diverse genus of orchids in Chile (Rodríguez *et al.* 2018), are pollinated exclusively by insects, especially Hymenoptera such as *Colletes* spp. and *Centris* spp., and Coleoptera such as *Astylus* spp. (Lehnebach & Riveros 2003; Humaña *et al.* 2008; Monzón *et al.* 2019).

In this study we studied pollinators in four *Chloraea* species, namely; *Chloraea collicensis*, *C. lamellata*, *C. crispa*, and *C. gavilu*. This information is essential to increase our understanding of Chilean orchid biology and their many interactions, which could contribute to their conservation, since some species are listed as endangered and most are not even evaluated (Novoa *et al.* 2015; Atala *et al.* 2017).

MATERIALS AND METHODS

Study area: Four *Chloraea* species were included in this study. *Chloraea collicensis* Kraenzl. and *C. lamellata* Lindl. were observed in a mixed population close to the city of Angol, Araucanía region (37°49'20" S, 72°41'30" W). The studied *C. crispa* Lindl. population was located in the Laja exit sector close to the main road, Biobío region (37°10'17'' S, 72°23'47" W). Lastly, *C. gavilu* Lidl. population was located in the Yumbel exit sector close to the main road, Biobío region (36°59'54.93" S, 72°34'24.10" W). *Chloraea collicensis* is recognized by some authors (Novoa *et al.* 2015), but is currently considered a synonym of *C. chrysochlora* Phil. (Rodríguez *et al.* 2018). However, there are no recent systematic studies of Chilean *Chloraea* species, highlighting the urgent need for a revision.

Study evaluation: During flowering, in November 2022, we conducted the field observations. These consisted in two visits per population separated by eight days. Observations were made in the morning and afternoon. We observed fully opened flowers of each species and registered presence of pollinators (Table 1). Sample size (n) was 50 flowers for *C. collicensis*, *C. lamellata* y *C. crispa* and 21 flowers for *C. gavilu*. Pollinators were captured and kept in polyethylene bags and were then transported to the laboratory for later identification. Insects, pretreated with acetone, were observed and photographed using a binocular scope (Olympus SZ2-ILST) with an attached digital camera (Moticam 2000). From direct observation and analysis of the digital photos, we identified the insect species according to morphological traits (Lazo 2015; MMA-ONU 2020). 30 days after capture of the pollinators, we evaluated in the field the percentage of formed capsules in order to assess the efficiency of natural pollination in these orchid species. To do this, we randomly selected 18 plants per species and we registered the total flowers, total formed capsules, and total aborted flowers.

Analysis data

Capsules formed percentages were calculated by dividing the number of capsules formed by the total number of flowers (×100). The normality distribution of the total number of flowers and percentages of capsules formed was evaluated with the D'Agostino & Pearson omnibus normality test. When the data were normally distributed a one-way ANOVA was used to test significance, followed by Tukey's post-hoc test at $P \leq 0.05$. Otherwise, a Kruskal-Wallis test was used to test significance, followed by Dunn's multiple comparisons test at $P \leq 0.05$. Statistical analyses were performed with the free software package R (Institute for Statistics and Mathematics 2022; https://www.r-project.org/).

RESULTS AND DISCUSSION

In this study, we found nine species of bees, ladybugs, bee flies, and small beetles visiting the four studied *Chloraea* species, from the Order Coleoptera (66.7 %) and Hymenoptera

(33.3 %) (Table 1, Fig. 1). Insects visiting the flowers were from 6 families; namely Bombyliidae (*Bombylius* sp.), Buprestidae (*Bilyaxia concinna*), Coccinellidae (*Eriopis connexa chilensis*), Melyridae (*Astylus trifasciatus*, *Arthrobrachus* sp.), Andrenidae (*Andrena crataegi*, *Andrena* sp.), and Miridae (*Gonzalezinus squamosus*). Only three of them were classified as potential pollinators (*Andrena* sp, *Andrena crategi*, and *Astylus trifasciatus*), as we detected attached pollinia in them (Table 1, Fig. 1), strongly suggesting their role as probable pollinators of these orchids. However, we cannot rule out that the other captured species of insects were visiting a flower which pollinia were already removed or that pollinia was lost when manipulating the samples for identification.

Most of these studies recorder diurnal pollinators, including the present study. There is evidence of nocturnal pollination in several orchid species (Pedron *et al.* 2012; Duque-Buitrago *et al.* 2014; Suetsugu *et al.* 2017). This syndrome has been associated with the form, color, and aroma of the flowers. Orchids pollinated during the day have usually evident visuals cues such as contrasting colors and notorious flowers (Koivisto *et al.* 2002). On the other hand, night-pollinated orchids can be usually white, cream-colored, or light yellow (Kelber *et al.* 2003), such as *C. collicensis* and *C. crispa*. Additionally, night-pollinated orchids commonly have strong scents as olfactory cues to guide pollinators (Martins & Johnson 2007; Suetsugu *et al.* 2017). In some species of the genus *Chloraea* scent glands have been described in the fleshy and thickened tips of the sepals, characteristics of the genus (Gumprecht 1980; Vogel 1990; Lehnebach 1999). Contrastingly, *C. gavilu* and *C. lamellata* have distinct yellow

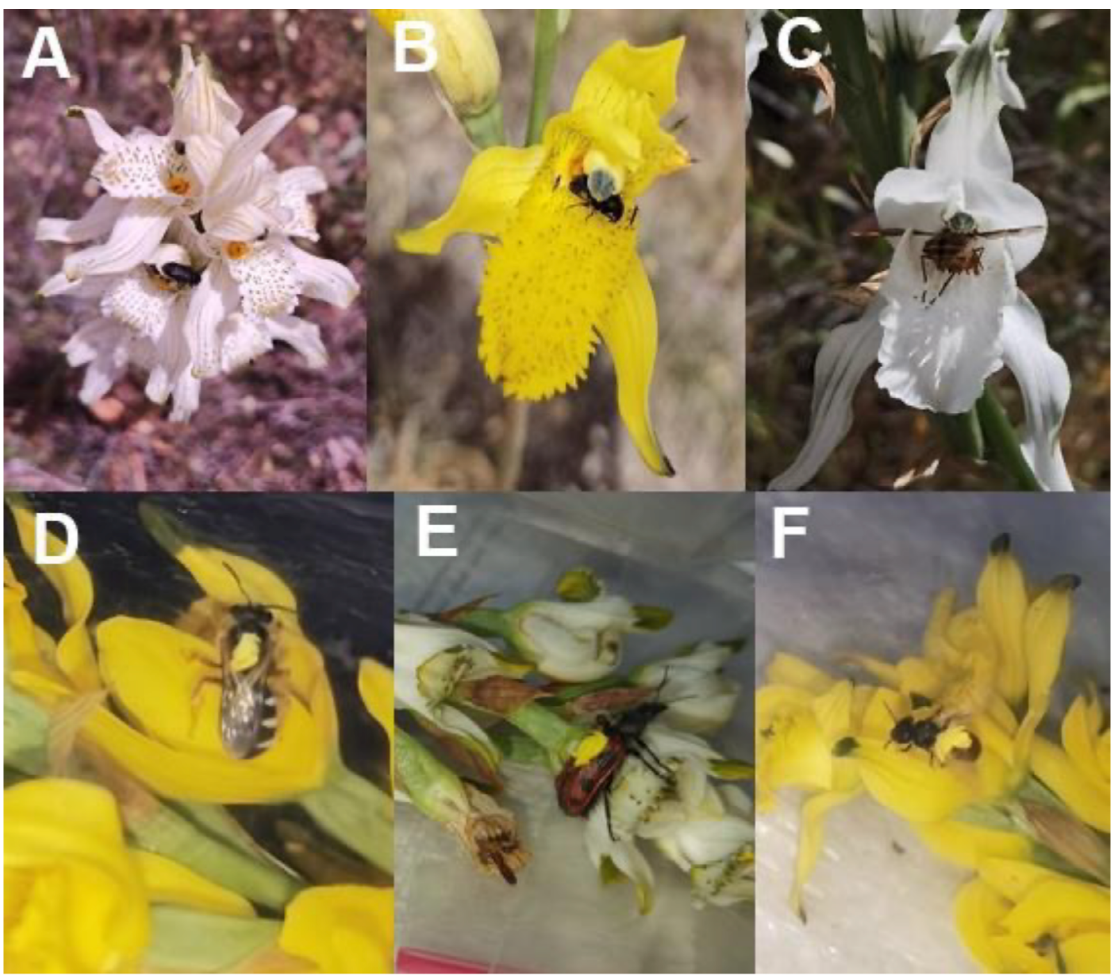

Figure 1. A-B *Chloraea collicensis* and *C. lamellata* visited by *Arthrobrachus* sp. C. *Bombylius* sp. in a *C. crispa* flower. D-F *Andrena* sp., *Astylus trafasciatus*, and *Andrena crataegi* with pollinia attached. / A-B. *Chloraea collicensis* y *C. lamellata* visitadas por *Arthrobrachus* sp. C. *Bombylius* sp atrapado en flor de *C. crispa*. D-F. *Andrena* sp., *Astylus trafasciatus*, and *Andrena crataegi* portando polinios.

flowers that contrasts with the green/brownish background, likely attracting daily pollinators via visual cues. The use of camera traps could provide confirmation of night-pollination in the two light-colored Chilean orchids. Numerous orchid species are pollinated by food deception, where rewardless flowers attract foraging pollinators through the mimicry of other flowers or the use of non-specific floral signals (Phillips & Batley 2020). We lack the information on nectar content and aromatic volatile emissions in these species to conclude on this regard.

Table 1. Floral visitors of four species of orchids of the genus *Chloraea*, endemic to the south-central zone of Chile, as potential pollinators. (*) marks the identified species with pollinia attached to them. / Visitantes florales de cuatro especies de orquídeas del género *Chloraea*, endémicas de la zona centro-sur de Chile, como potenciales polinizadores. (*) marca las especies identificadas con polinias adheridas.

Order	Family	Genus/species	*C. collicensis*	*C. crispa*	*C. gavilu*	*C. lamellata*
Coleoptera	Bombyliidae	*Bombylius sp*		x	x	
	Buprestidae	*Bilyaxia concinna*				x
	Coccinellidae	*Eriopis connexa chilensis*		x	x	
	Melyridae	*Astylus trifasciatus*	x*			
		Arthrobrachus sp			x	x
		Gonzalezinus squamosus	x	x		
Hymenoptera	Andrenidae	*Andrena crataegi*				x*
		Andrena sp				x*
	Miridae	*Gonzalezinus squamosus*	x	x		

All orchid species were equally visited, with no evidence of specificity among them. Despite pollinator visits apparently not being species-specific, insect visitation frequency was low and fruit-set scant. Despite the fact that we cannot functionally connect insect visits to capsule formation in this study, the observed results suggest that fruit set in these species could be limited by pollinators. Overall, the recorded diversity and abundance of potential pollinators was relatively low. The low pollination rates typical for orchids are generally attributed to pollinator limitation, i.e. the absence or rarity of pollinators (Wilcock & Neiland 2002; Tremblay *et al.* 2005). In this study, it may be due to the fact that strong winds are common in the study site and there is also presence of invasive plant species such as *Rubus* sp., *Genista monspessulana*, *Echium vulgare*, among others. These species have been known to negatively impact native plant pollination by capturing the pollination service with a greater floral display (Lehnebach & Riveros 2003; Carvallo *et al.* 2013; Carvallo & Medel 2016). Additionally, the introduction of exotic insect species have reduce the populations of many native insects (Sanguinetti & Bustos 2014). Such is the case of the native bumblebee (*Bombus dahlbomii*) that is now severely threatened by the introduction of the exotic *Bombus terrestris* (Fonturbel *et al.* 2023).

In the field, over 60 % of all flowers aborted, even in some cases the totality of the flowers of an individual were aborted. Capsule production (natural pollination) in the field was low for all studied species, with values not exceeding 35 %. Nevertheless, low capsule production by natural pollination has been reported for other species of the genus (Lehnebach & Riveros 2003; Humaña *et al.* 2008; Cuartas-Domínguez & Medel 2010). There is also no significant difference in the average number of fertilized flowers across species (Fig. 2). *C. lamellata* presented the lower capsule formation percentage, reaching only 22.5 %. This is in line with another studied species in the area, *C. disoides* (22 % capsule formation, Pereira *et al.* unpublished data). Reproductive failure in plants can often be attributed to pollination limitation, as stated above, where the movement of viable pollen between flowers through the absence of pollinators is insufficient (Bierzychudek 1981; Zimmerman & Pyke 1988). Species of the genus *Chloraea* are usually pollinator-dependent for fruit set, requiring the presence of pollen on the stigma as a stimulus as seen in other temperate orchids (Neiland

& Wilcock 1998), and self-pollination is morphologically prevented in most orchids by the herkogamous structure of flowers (Proctor *et al.* 1996). Self-pollination has been tested in *C. lamellata* (Lehnebach & Riveros 2003), *C. crispa* (Humaña *et al*. 2008) and *C. gavilu* (Pereira *et al.* unpublished data). In all cases, cross-pollination resulted in higher capsule formation. This further underlines the importance of natural pollinators for the long-term conservation of orchid species. The need is not to preserve only threatened orchids, such as *C. disoides* (Atala *et al.* 2017), but also their natural environments, where their pollinators and mutualistic fungi reside. Lastly, further studies, including night pollinators, should be conducted to further the knowledge on Chilean orchid pollinators, strategies, and pollination ecology. This information could be essential for effective management and conservation decisions and strategies.

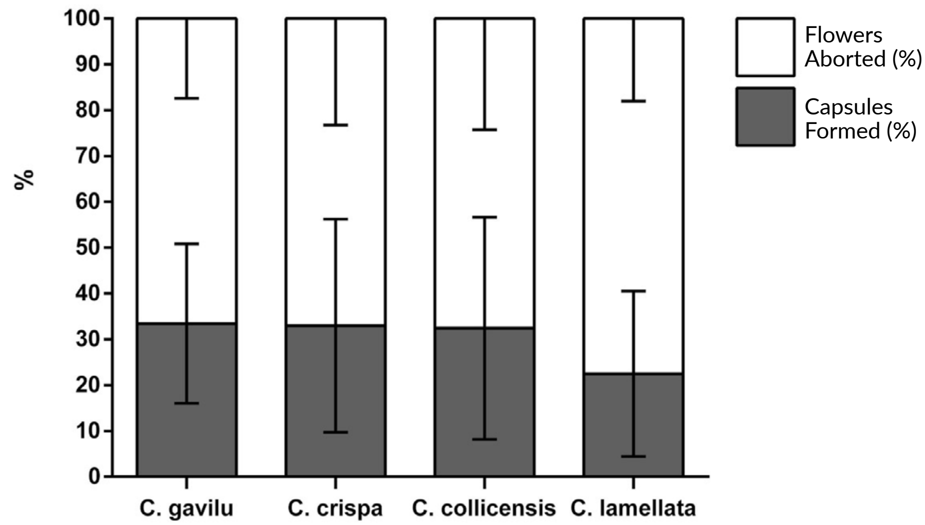

Figure 2. Percentage of flowers aborted and capsules formed in *C. gavilu*, *C. crispa*, *C. collicensis*, and *C. lamellata.*. No significant difference between columns were detected (1-way ANOVA, P > 0.05). / Porcentaje de flores abortadas y cápsulas formadas en *C. gavilu*, *C. crispa*, *C. collicensis*, *y C. lamellata*. No se detectaron diferencias significativas entre columnas (ANOVA de 1 vía, P > 0,05).

ACKNOWLEDGEMENTS

The authors declare that this research was not funded by any external entity.

REFERENCES

Atala, C., Muñoz-Tapia, L., Pereira, G., Romero, C., Vargas, R., Acuña-Rodriguez, I.S., Molina-Montenegro, M.A., Brito, E. 2017. The effect of future climate change on the conservation of *Chloraea disoides* Lindl. (Orchidaceae) in Chile. Brazilian Journal of Botany 40: 353-360. https://doi.org/10.1007/s40415-016-0333-4

Bierzychudek, P. 1981. Pollinator Limitation of Plant Reproductive Effort. The American Naturalist 117(5): 838-840. https://doi.org/10.1086/283773

Carvallo, G., Medel, R. 2016. Heterospecific pollen transfer from an exotic plant to native plants: assessing reproductive consequences in an Andean grassland. Plant Ecology & Diversity 9(2): 151-157. https://doi.org/10.1080/17550874.2016.1140243

Carvallo, G., Medel, R., Navarro, L. 2013. Assessing the effects of native plants on the pollination of an exotic herb, the blueweed *Echium vulgare* (Boraginaceae). Arthropod-Plant Interactions 7: 475-484. https://doi.org/10.1007/s11829-013-9265-0

Cozzolino, S., Widmer, A. 2005. The evolutionary basis of reproductive isolation in Mediterranean orchids. Taxon 54: 977-985. https://doi.org/10.2307/25065482

Cuartas-Domínguez, M., Medel, R. 2010. Pollinator-mediated selection and experimental manipulation of the flower phenotype in *Chloraea bletioides*. Functional Ecology 24: 1219-1227. https://doi.org/10.1111/j.1365-2435.2010.01737.x

Dressler, RL. 1993. Phylogeny and classification of the orchid family. Cambridge University Press, Cambridge.

Duque-Buitrago, C., Alzate-Quintero, N., Otero, J. 2014. Nocturnal pollination by fungus gnats of the Colombian endemic species, *Pleurothallis marthae* (Orchidaceae: Pleurothallidinae). Lankesteriana: International Journal on Orchidology 13: 3. https://doi.org/10.15517/lank.v13i3.14429

Fontúrbel, F.E., Sepúlveda, I.B., Muschett, G., Carvallo, G., Vieli, L., Murúa, M.M. 2023. Do exotic plants and flower colour facilitate bumblebee invasion? Insights from citizen science data. Flora: Morphology, Distribution, Functional Ecology of Plants 298: 152200. https://doi.org/10.1016/j.flora.2022.152200

Gumprecht, R. 1980. Blossom structure and pollinating mechanism in endemic orchids of South America. Medio Ambiente 4: 99-103.

Hawkeswood, T.J., Turner, J.R. 2004. Observations on *Metriorrhynchus rhipidius* (Macleay) (Coleoptera: Lycidae) feeding on nectar from the flowers of *Leucopogon muticus* R. Br. (Epacridaceae) at Kenthurst, New South Wales, Australia. Calodema 2: 8-10.

Herrera, C.M., Castellanos, M.C., Medrano, M. 2006. Geographical context of floral evolution: towards an improved research programme in floral diversification. In: Harder, L.D., Barrett, S.C. (Eds.). Ecology and Evolution of Flowers, pp. 278-294. Oxford University Press. https://doi.org/10.1093/oso/9780198570851.003.0015

Heywood, V., Brummitt, R., Culham, A., Seberg, O. 2007. Flowering plant families of the world. Firefly Books: Ontario, Canada.

Humaña, A., Cisternas, M., Valdivia, C. 2008. Breeding system and pollination of selected orchids of the genus *Chloraea* (Orchidaceae) from central Chile. Flora - Morphology, Distribution, Functional Ecology of Plants 203(6): 469-473. https://doi.org/10.1016/j.flora.2007.08.004

Johnson, S.D., Steiner, K.E. 2000. Generalization versus specialization in plant pollination systems. Trends in Ecology & Evolution 15(4): 140-143. https://doi.org/10.1016/S0169-5347(99)01811-X

Kaur, S. 2019. Orchids and Pollination. Acta Scientific agriculture 3(8): 160-163. https://doi.org/10.31080/ASAG.2019.03.0579

Kelber, A., Balkenius, A., Warrant, E.J. 2003. Colour Vision in Diurnal and Nocturnal Hawkmoths, Integrative and Comparative Biology 43(4): 571-579. https://doi.org/10.1093/icb/43.4.571

Koivisto, A-M., Vallius, E., Salonen, V. 2002. Pollination and reproductive success of two colour variants of a deceptive orchid, *Dactylorhiza maculata* (Orchidaceae). Nordic Journal of Botany 22(1): 53-58. https://doi.org/10.1111/j.1756-1051.2002.tb01621.x

Lazo, W. 2015. Insectos de Chile: Atlas entomológico. Editorial Universidad de Chile. Santiago, Chile.

Lehnebach, C.A. 1999. Current status of the Chilean Orchid Flora. Orchid Conservation News, Orchid Specialist Group IUCN/SSC 2: 8-10.

Lehnebach, C.A. 2003. Pollination biology of the Chilean endemic orchid *Chloraea lamellata*. Biodiversity and Conservation 12(8): 1741-1751. https://doi.org/10.1023/A:1023666800948

Lehnebach, C., Robertson, A. 2004. Pollination Ecology of Four Epiphytic Orchids of New Zealand. Annals of Botany 93: 773-781. https://doi.org/10.1093/aob/mch097

MMA-ONU Medio Ambiente. 2020. Guía de Bolsillo: Insectos Polinizadores Nativos de la Zona Central de Chile. Santiago, Chile.

Martins, D.J., Johnson, S.D. 2007. Hawkmoth pollination of aerangoid orchids in Kenya, with special reference to nectar sugar concentration gradients in the floral spur. American Journal of Botany 94: 650. https://doi.org/10.3732/ajb.94.4.650

Micheneau, C., Johnson, S.D., Fay, M.F. 2009. Orchid pollination: from Darwin to the present day. Botanical Journal of the Linnean Society 161: 1-19. https://doi.org/10.1111/j.1095-8339.2009.00995.x

Micheneau, C., Fournel, J., Warren, B.H., Hugel, S., Gauvin-Bialecki, A., Pailler, T., Strasberg, D., Chase, M.W. 2010. Orthoptera, a new order of pollinator. Annals of Botany 105(3): 355-364. https://doi.org/10.1093/aob/mcp299

Monzón, V., Araujo, R., Avendaño, P., Garrido, R., Mesquita-Neto, J. 2019. Discovering new floral visitors of four Chilean endemic orchids. Gayana 83(2) 141-144. https://doi.org/10.4067/S0717-65382019000200141

Neiland, M., Wilcock, C. 1998. Fruit set, nectar reward, and rarity in the Orchidaceae. American Journal of Botany 85: 1657-1671. https://doi.org/10.2307/2446499

Newman, E., Anderson, B., Johnson, S.D. 2011. Flower colour adaptation in a mimetic orchid. Proceedings of the Royal Society B: Biological Sciences 279: 2309-2313. https://doi.org/10.1098/rspb.2011.2375

Novoa, P., Espejo, J., Alarcón, D., Cisternas, M., Domínguez, E. 2015. Guía de Campo de las Orquídeas Chilenas. Segunda edición. Ed. Corporación Chilena de la Madera, Concepción, Chile. 244 p.

Pedron, M., Buzatto, C.R., Singer, R.B., Batista, J.A.N., Moser, A. 2012. Pollination biology of four sympatric species of *Habenaria* (Orchidaceae: Orchidinae) from southern Brazil. Botanical Journal of the Linnean Society 170: 141-156. https://doi.org/10.1111/j.1095-8339.2012.01285.x

Phillips, R.D., Batley, M. 2020. Evidence for a food-deceptive pollination system using Hylaeus bees in *Caladenia hildae* (Orchidaceae). Australian Journal of Botany 68(2): 146-152. https://doi.org/10.1071/BT20002

Proctor, M., Yeo, P., Lack, A. 1996. The Natural History of Pollination. Timber Press, Portland, Oregon.

Ramírez, S., Gravendeel, B., Singer, R., Marshall, C., Pierce, N. 2007. Dating the origin of the Orchidaceae from a fossil orchid with its pollinator. Nature 448(30): 1042- 1045. https://doi.org/10.1038/nature06039

Rasmussen, H.N. 2002. Recent developments in the study of orchid mycorrhiza. Plant and Soil 244: 149-163. https://doi.org/10.1023/A:1020246715436

Reina-Rodríguez, G., Ospina-Calderón, N., Castaño, A., Soriano, I., Otero, J. 2010. Listado de las orquídeas del Valle del río Cauca y su piedemonte andino (930-1200 m.s.n.m) Sur-occidente colombiano. Cespedesia 32(90-91): 7-22.

Roberts, D.L. 2003. Pollination biology: The role of sexual reproduction in orchid conservation. In: Dixon, K.W., Kell, S.P., Barrett, R.L., Cribb, P.J. (Eds.) Orchid Conservation, pp. 113-136. Natural History Publications, Kota Kinabalu, Sabah, Malaysia. ISBN 978-983-812-078-4.

Sanguinetti, A., Bustos, R. 2014. Invasive bees promote high reproductive success in Andean orchids. Biological Conservation 175: 10-20. https://doi.org/10.1016/j.biocon.2014.04.011

Schiestl, F., Schluter, P. 2009. Floral isolation, specialized pollination, and pollinator behavior in orchids. Annual Review of Entomology 54: 425-446. https://doi.org/10.1146/annurev.ento.54.110807.090603

Scopece, G., Schiestl, F., Cozzolino, S. 2014. Pollen transfer efficiency and its effect on inflorescence size in deceptive pollination strategies. Plant Biology 7(2): 545-550. https://doi.org/10.1111/plb.12224

Statman-Weil, Z. 2001. Aedes communis: The Pollinating Mosquito. US Forest Service, Washington DC, USA.

Stökl, J., Brodmann, J., Dafni, A., Ayasse, M., Hansson, B.S. 2011. Smells like aphids: Orchid flowers mimic aphid alarm pheromones to attract hoverflies for pollination. Proceedings of the Royal Society B: Biological Sciences 278: 1216-1222. https://doi.org/10.1098/rspb.2010.1770

Suetsugu, K., Nakahama, N., Ito, A., Isagi, Y. 2017. Time-lapse photography reveals the occurrence of unexpected bee-pollination in *Calanthe izuinsularis*, an endangered orchid endemic to the Izu archipelago. Journal of Natural History 51:13-14. https://doi.org/10.1080/00222933.2017.1293745

Tremblay, R., Ackerman, J., Zimmerman, J., Calvo, R. 2005. Variation in sexual reproduction in orchids and its evolutionary consequences: a spasmodic journey to diversification. Biological Journal of the Linnean Society 84: 1-54. https://doi.org/10.1111/j.1095-8312.2004.00400.x

Tremblay, R. 1992. Trends in the pollination ecology of the Orchidaceae: evolution and systematics. Canadian Journal of Botany 70(3): 642-650. https://doi.org/10.1139/b92-083

Vogel, S. 1990. The Role of Scent Glands in Pollination. Amerind Publishing Pvt. Ltd, New Delhi, India.

Wilcock, C., Neiland, R. 2002. Pollination failure in plants: why it happens and when it matters. Trends in Plant Science 7(6): 270-277. https://doi.org/10.1016/S1360-1385(02)02258-6

Zimmerman, M., Pyke, G.H. 1988. Reproduction in Polemonium: assessing the factors limiting seed set. The American Naturalist 131: 723-738. https://doi.org/10.1086/284815

Received: 22.08.2024
Accepted: 08.05.2025

Editor: Alfredo Saldaña