

AN OVERVIEW OF THE KNOWLEDGE OF THE ORCHIDACEAE IN THE STATE OF AMAZONAS, BRAZILIAN AMAZON

UMA VISÃO GERAL DO CONHECIMENTO SOBRE ORCHIDACEAE NO ESTADO DO AMAZONAS, AMAZÔNIA BRASILEIRA

PANORAMA GENERAL DEL CONOCIMIENTO SOBRE LAS ORCHIDACEAE EN EL ESTADO DE AMAZONAS, AMAZONÍA BRASILEÑA

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ABSTRACT: This study provides an updated synthesis of Orchidaceae in Amazonas, Brazil, focusing on taxonomy, diversity, endemism, distribution, natural hybrids, reproductive biology, anatomy, ecology, and conservation. Data from *Flora e Funga do Brasil*, updated to June 2026, were complemented by specialized literature. A total of 457 species in 109 genera are recognized, representing 18.18% of Brazilian and 58.29% of Brazilian Amazonian species. Of these, 116 are endemic to Brazil, including 110 in Epidendroideae, the richest subfamily in Amazonas (401 spp.), particularly in Cymbidieae and Epidendreae. *Epidendrum*, *Maxillaria* and *Catasetum* are among the richest genera. Despite its high diversity, knowledge remains spatially and taxonomically uneven, emphasizing the need for further field inventories, taxonomic and ecological studies, herbarium analyses, and conservation assessments, especially in poorly sampled areas.

Keywords: Taxonomic Diversity. Flora of Amazonas. Orchids. Neotropical Region. Species Richness.

RESUMO: Este estudo apresenta uma síntese atualizada do conhecimento sobre Orchidaceae no Amazonas, Brasil, com foco em taxonomia, diversidade, endemismo, distribuição, híbridos naturais, biologia reprodutiva, anatomia, ecologia e conservação. Dados da *Flora e Funga do Brasil*, atualizados até junho de 2026, foram complementados por literatura especializada. São reconhecidas 457 espécies em 109 gêneros, correspondendo a 18,18% das espécies brasileiras e 58,29% das espécies da Amazônia brasileira. Destas, 116 são endêmicas do Brasil, incluindo 110 pertencentes a Epidendroideae, a subfamília mais diversa no Amazonas (401 spp.), especialmente nas tribos Cymbidieae e Epidendreae. *Epidendrum*, *Maxillaria* e *Catasetum* estão entre os gêneros mais ricos. Apesar da elevada diversidade, o conhecimento permanece espacial e taxonomicamente desigual, reforçando a necessidade de ampliar inventários de campo, estudos taxonômicos e ecológicos, análises de herbários e avaliações de conservação, especialmente em áreas pouco amostradas.

Palavras-chave: Diversidade Taxonômica. Flora do Amazonas. Orquídeas. Região Neotropical. Riqueza de Espécies.

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RESUMEN: Este estudio presenta una síntesis actualizada del conocimiento sobre Orchidaceae en Amazonas, Brasil, con énfasis en taxonomía, diversidad, endemismo, distribución, híbridos naturales, biología reproductiva, anatomía, ecología y conservación. Los datos de *Flora e Funga do Brasil*, actualizados hasta junio de 2026, fueron complementados con literatura especializada. Se reconocen 457 especies en 109 géneros, correspondientes al 18,18% de las especies brasileñas y al 58,29% de las especies registradas para la Amazonía brasileña. De estas, 116 son endémicas de Brasil, incluyendo 110 pertenecientes a Epidendroideae, la subfamilia más diversa de Amazonas (401 spp.), especialmente en las tribus Cymbidieae y Epidendreae. *Epidendrum*, *Maxillaria* y *Catasetum* se encuentran entre los géneros más diversos. A pesar de su elevada diversidad, el conocimiento permanece espacial y taxonómicamente desigual, lo que refuerza la necesidad de ampliar los inventarios de campo, los estudios taxonómicos y ecológicos, los análisis de herbarios y las evaluaciones de conservación, especialmente en áreas poco muestreadas.

Palabras clave: Diversidad Taxonómica. Flora Del Amazonas. Orquídeas. Región Neotropical. Riqueza de Especies.

INTRODUCTION

Orchidaceae was formally recognized by Jussieu (1789), with its name derived from the Greek *orchis*, referring to the tubers of *Orchis* L.; the genus was established by Linnaeus (1753). Despite generally recognizable flowers, Orchidaceae exhibits remarkable morphological diversity, with floral structures often modified, reduced or fused, complicating identification (Dressler, 1993).

Orchids display diverse habits and growth forms, including epiphytic, terrestrial, aquatic, hemiepiphytic, rupicolous and mycoheterotrophic species. Their roots commonly possess velamen and mycorrhizal associations, while stems, leaves and inflorescences show considerable variation. Flowers are typically zygomorphic, with a differentiated labellum, gynostemium and pollinia, and fruits contain numerous wind-dispersed, endosperm-free seeds (Dressler, 1993; Souza; Lorenzi, 2008).

Orchidaceae is currently the largest angiosperm family, with 28,000–31,000 species (Christenhusz; Byng, 2016). Phylogenetic studies recognize 49 subtribes (Pridgeon, et al., 1999, 2001, 2003, 2005, 2009, 2014; Chase, et al., 2015), while molecular studies continue to revise generic circumscriptions (e.g. Neubig, et al., 2012; Karremans, et al., 2016; Smidt, et al., 2021a, 2021b; Pérez-Escobar, et al., 2022; Meneguzzo; Chase, 2024a, 2024b). Consequently, approximately 700–736 genera are currently recognized (Chase, et al., 2015; Pessoa, et al., 2025).

The Neotropics represent a major diversity center, with about 300 genera and more than 8,000 species, particularly concentrated in the Andes, Central America and Atlantic Forest

(Dressler, 1981; Carmona-Higueta, et al., 2025). Orchidaceae also dominates Neotropical vascular epiphyte diversity, accounting for 8,097 species and 83% of endemic epiphytes (Carmona-Higueta, et al., 2025).

Brazil is among the world's richest countries for Orchidaceae, with 2,515 accepted species in 207 genera, including 1,540 endemics (BFG, 2022; Pessoa, et al., 2025). It follows Colombia and Ecuador, with approximately 4,600 and 4,000 species, respectively (Dressler, 1981; Pérez-Escobar, et al., 2022; Ulloa; Neill, 2005; Christenhusz; Byng, 2016). Despite this diversity, major knowledge gaps remain, particularly in the Amazon and Amazonas, where collections are sparse and concentrated near urban centers (Pessoa, et al., 2025).

Therefore, this review summarizes current knowledge of Orchidaceae in Amazonas, focusing on diversity, richness, endemism, taxonomy, systematics and natural hybrids, while also addressing reproductive biology, anatomy, ecology and conservation.

METHODOLOGY

Most data, including genera and species checklists, richness, geographic distribution, and endemism, were obtained from *Flora e Funga do Brasil* (<https://floradobrasil.jbrj.gov.br/consulta/#CondicaoTaxonCP>), a collaborative project initiated in 2008. The platform was consulted regularly from May to early August 2026, and data updated through June 2026 were systematically compiled. Information on accepted names, genera, taxonomic status, distribution, endemism, and available taxonomic and nomenclatural data was extracted and checked for consistency.

A complementary literature survey was conducted from May to early August 2026 using Google Scholar, Web of Science, Scopus, SciELO, JSTOR and Biodiversity Heritage Library (BHL). Searches used “Amazonas”, “Orchidaceae”, and “orchids”, individually and in combinations such as “Amazonas” AND “Orchidaceae”, “Amazonas” AND “orchids”, and taxon names, in Portuguese, English and Spanish. Eligible publications included floristic surveys, taxonomic and nomenclatural studies, new taxa, distribution records, conservation assessments, checklists and natural hybrids. Duplicates were identified using title, authors, publication year and DOI and removed.

Selected publications were reviewed for taxonomic identity, synonyms, occurrence, distribution, new records, range extensions, endemism, natural hybrids and conservation information. Taxonomic data were cross-checked against *Flora e Funga do Brasil*. Species

richness was based on accepted taxa for Amazonas, while endemic species were defined as those restricted to the state according to *Flora e Funga do Brasil* and, when necessary, the taxonomic literature. New occurrences and range extensions were recognized from documented records not previously reported in the consulted literature. Natural hybrids were treated separately and included only when formally recognized.

The compiled data were standardized and synthesized to identify patterns of richness, distribution, endemism and taxonomic change. Knowledge gaps were qualitatively identified based on taxonomic groups, species, geographic areas or other aspects for which information was scarce, outdated or absent. These patterns were used to assess persistent knowledge gaps and the current state of knowledge and conservation of Orchidaceae in Amazonas.

ORCHIDACEAE IN THE BRAZILIAN AMAZON: FOCUS ON AMAZONAS

Orchidaceae is the second richest family in the Brazilian Amazon, with 134 genera and 784 native or naturalized species, including 517 restricted to the Amazon Forest; epiphytic, hemiepiphytic and climbing species predominate (608 spp.), followed by terrestrial, rupicolous and marshy species (176 spp.). *Catasetum* Rich. ex Kunth, *Epidendrum* L., *Habenaria* Willd. and *Maxillaria* Ruiz & Pav. are among the richest genera, while Catasetinae, Laeliinae and Pleurothallidinae are particularly diverse (Pessoa, et al., 2025).

Despite numerous floristic and taxonomic studies, research remains insufficient relative to the region's extent and diversity (Pessoa, et al., 2025). Floristic inventories include Silva et al. (1995), Silveira et al. (1995), Atzingen et al. (1996), Cardoso et al. (1996), Koch et al. (2014), Luz et al. (2016) and Nóbrega et al. (2016). Taxonomic studies include Braga (1977a), Cruz (1994), Cruz & Braga (1997), Batista et al. (2008), Monteiro et al. (2009), Carneiro-Silva et al. (2015), Pessoa et al. (2015), Afonso et al. (2016), Cantuária (2017), Koch et al. (2018) and Klein & Piedade (2019).

More recent contributions include Krahll (2020), Cantuária et al. (2021), Ferreira-Filho et al. (2021), Ferreira-Filho & Barberena (2022) and Costa & Barberena (2023). In Amazonas, continued new records (e.g., Pessoa, et al., 2013; Krahll, et al., 2014a, 2014b; Valsko, et al., 2014a; Krahll, et al., 2015a, 2020a, 2020b, 2021a, 2021b, 2022a, 2025a, 2025b) and newly described species and nothospecies (e.g., Braga, 1977b, 1978; Miranda, 1988; Silva; Oliveira, 1998a, 1998b; Campacci; Silva, 2008; Pessoa, et al., 2014; Valsko, et al., 2014b, 2014c; Krahll, et al., 2015b; Pessoa; Alves, 2015; Krahll, et al., 2016a, 2016b; Petini-Benelli, 2016; Valsko, et al., 2019; Hágsater;

Cordeiro, 2020; Hágsater; Krahll, 2020; Hágsater; Wrazidlo, 2020; Krahll, et al., 2020c; Pessoa; Karremans, 2022; Krahll, et al., 2021c, 2021d, 2022b, 2022c, 2023a, 2023b, 2023c, 2024a, 2025c, 2025d, 2025e) demonstrate persistent taxonomic gaps. Only five studies have focused exclusively on Orchidaceae taxonomy in Amazonas: Braga (1977a), Cruz (1994), Cruz & Braga (1997), Klein et al. (2019) and Krahll (2020). Of these, only Braga (1977a) and Krahll (2020) were conducted around Manaus, indicating a strong spatial imbalance in research efforts.

TAXONOMIC OVERVIEW OF ORCHIDACEAE IN THE STATE OF AMAZONAS

Based mainly on the classification of Chase et al. (2015), data from *Flora e Funga do Brasil* (BFG, 2015, 2018, 2022), and specialized literature, Amazonas harbors 457 Orchidaceae species in 109 genera, representing 18.18% of Brazilian species and 58.29% of those recorded in the Brazilian Amazon (Pessoa, et al., 2025).

Of these, 116 species (25.38%) are endemic to Amazonas, with Epidendroideae accounting for 110 species (94.8% of state endemism). Four subfamilies occur in Brazil and Amazonas: Vanilloideae, Cypridioideae, Orchidoideae and Epidendroideae (Chase et al., 2015; Pessoa, et al., 2025). Epidendroideae is by far the richest, with 401 species, particularly *Epidendrum* L. (40 spp.), *Maxillaria* Ruiz & Pav. (39 spp.), *Catasetum* Rich. ex Kunth (38 spp.), *Dichaea* Lindl. (17 spp.), *Octomeria* R. Br. (13 spp.), *Sobralia* Ruiz & Pav. (11 spp.), *Anathallis* Barb. Rodr. (10 spp.) and *Coryanthes* Hook. (10 spp.). Its richest tribes are Cymbidieae (215 spp.) and Epidendreae (143 spp.), while the remaining eight tribes each have fewer than 20 species. Epidendroideae also includes the only two mycoheterotrophic species in Amazonas, *Uleiorchis ulei* and *Wulfschlaegelia calcarata*, belonging to Gastrodieae and Wulfschlaegeliae, respectively.

Orchidoideae is the second richest subfamily, with 35 terrestrial species, including 21 *Habenaria* Willd. species (60%). Its other representatives belong to Cranichideae: Cranichidinae (1 sp.), Goodyerinae (6 spp.) and Spiranthininae (7 spp.).

Vanilloideae comprises 20 terrestrial, epiphytic or hemiepiphytic species. Vanilleae includes 14 species of *Epistephium* Kunth and *Vanilla* Mill.; although *V. planifolia* Andrews is the main commercial vanilla species (Rain, 2004), it does not naturally occur in Amazonas. Pogonieae is represented by *Cleisthes* Rich. ex Lindl. and *Duckeella* Porto & Brade.

The taxonomic composition and species richness of Orchidaceae in Amazonas are summarized in Table 1.

Table 1. Orchidaceae species recorded in Amazonas by subfamily, tribe, subtribe and genus, following Chase et al. (2015). Numbers in parentheses indicate total and endemic species. N/A: not applicable.

Subfamilies	Tribes	Subtribes	Genera
Vanilloideae (20/4)	Pogonieae (6)	N/A	<i>Cleisthes</i> (3/0) <i>Duckeella</i> (3/2)
	Vanilleae (14)	N/A	<i>Epistephium</i> (4/1) <i>Vanilla</i> (10/1)
Cypripedioideae (2/0)	N/A	N/A	<i>Phragmipedium</i> (1/0) <i>Selenipedium</i> (1/0)
Orchidoideae (35/2)	Cranichideae (14)	Cranichidinae (1)	<i>Prescottia</i> (1/0)
		Goodyerinae (6)	<i>Aspidogyne</i> (2/0) <i>Microchilus</i> (4/1)
		Spiranthinae (7)	<i>Beloglottis</i> (1/0) <i>Cyclopogon</i> (1/0) <i>Eltroplectris</i> (1/0) <i>Helonoma</i> (1/0) <i>Pelexia</i> (1/0) <i>Sarcoglottis</i> (2/1)
	Orchideae (21)	Habenariinae (21)	<i>Habenaria</i> (21/0)
Epidendroideae (401/110)	Cymbidieae (215)	Catasetinae (54)	<i>Catasetum</i> (38/15) <i>Clowesia</i> (2/1) <i>Cynoches</i> (3/0) <i>Galeandra</i> (3/0) <i>Mormodes</i> (8/5)
		Coeliopsidinae (2)	<i>Peristeria</i> (2/0)

Cyrtopodiinae (2)

Cyrtopodium (2/o)

Eriopsidinae (2)

Eriopsis (2/1)

Eulophiinae (2)

Eulophia (1/o)

Oeceoclades (1/o)

Maxillariinae (46)

Bifrenaria (6/2)

Maxillaria (39/4)

Xylobium (1/o)

Oncidiinae (50)

Aspasia (1/o)

Brassia (4/o)

Erycina (3/o)

Gomesa (1/o)

Ionopsis (2/o)

Lockhartia (1/o)

Macradenia (2/o)

Macroclinium (2/o)

Notylia (7/2)

Oncidium (4/2)

Ornithocephalus (3/o)

Otoglossum (1/1)

Plectrophora (2/o)

Polyotidium (1/1)

Quekettia (2/1)

Rodriguezia (7/2)

Solenidium (1/o)

Trichocentrum (5/o)

Trichopilia (1/o)

Stanhopeinae (23)

Acineta (1/o)

Braemia (1/o)

Coryanthes (10/4)

Gongora (5/2)

Houlletia (1/o)

Lueckelia (1/o)

Paphinia (1/1)

Polycynis (2/o)

Stanhopea (1/o)

Zygopetalinae (32)

Aganisia (3/o)

Batemannia (1/o)

		<i>Cryptarrhena</i> (2/o)
		<i>Dichaea</i> (17/4)
		<i>Galeottia</i> (3/3)
		<i>Koellensteinia</i> (2/1)
		<i>Otostylis</i> (1/o)
		<i>Warczewiczella</i> (1/o)
		<i>Weidmannia</i> (1/o)
		<i>Zygosepalum</i> (1/o)
Epidendrae (143)		
	Laeliinae (81)	
		<i>Brassavola</i> (4/2)
		<i>Cattleya</i> (4/o)
		<i>Caularthron</i> (1/o)
		<i>Dimerandra</i> (1/o)
		<i>Encyclia</i> (9/1)
		<i>Epidendrum</i> (40/12)
		<i>Jacquinella</i> (2/o)
		<i>Laelia</i> (2/1)
		<i>Nidema</i> (1/o)
		<i>Orleanesia</i> (5/3)
		<i>Prosthechea</i> (3/1)
		<i>Scaphyglottis</i> (9/1)
	Pleurothallidinae (62)	
		<i>Acianthera</i> (7/2)
		<i>Anathallis</i> (10/6)
		<i>Dryadella</i> (1/o)
		<i>Echinosepala</i> (2/1)
		<i>Karma</i> (3/2)
		<i>Lepanthes</i> (1/o)
		<i>Masdevallia</i> (3/1)
		<i>Madisonia</i> (2/1)
		<i>Muscarella</i> (2/o)
		<i>Myoxanthus</i> (1/1)
		<i>Niphanta</i> (1/o)
		<i>Octomeria</i> (13/5)
		<i>Pabstiella</i> (1/o)
		<i>Pleurothallis</i> (3/2)
		<i>Specklinia</i> (2/o)
		<i>Stelis</i> (6/1)
		<i>Trichosalpinx</i> (3/1)
		<i>Trisetella</i> (1/1)
Gastrodieae (1)		
	N/A	
		<i>Uleiorchis</i> (1/o)

Malaxideae (6)	Dendrobiinae (4)	<i>Bulbophyllum</i> (4/1)
	Malaxidinae (2)	<i>Liparis</i> (1/0) <i>Malaxis</i> (1/0)
Nottieae (6)	N/A	<i>Palmorchis</i> (6/1)
Sobralieae (17)	N/A	<i>Eleanthus</i> (6/3) <i>Sobralia</i> (11/2)
Triphoreae (2)	Triphorinae (2)	<i>Triphora</i> (2/0)
Vandae (10)	Angraecinae (8)	<i>Campylocentrum</i> (8/2)
	Polystachynae (2)	<i>Polystachya</i> (2/0)
Wulschlaegelieae (1)	N/A	<i>Wulschlaegelia</i> (1/0)
Xerorchideae (2)	N/A	<i>Xerorchis</i> (2/0)

Source: prepared by A.H. Krahel and D.R.P. Krahel

The following sections summarize recent studies on each subfamily, emphasizing species richness, distribution, and relevant taxonomic aspects in Amazonas.

APOSTASIOIDEAE

No species of this subfamily have been recorded in Brazil (Pessoa, et al., 2025).

VANILLOIDEAE

The subfamily Vanilloideae comprises 14 genera, including four occurring in Brazil and Amazonas: *Cleisthes* Rich. ex Lindl., *Duckeella* Porto & Brade, *Epistephium* Kunth and *Vanilla* Mill. (Pridgeon, et al., 2001; Chase, et al., 2015; Pessoa et al., 2025). Vanilleae is represented in Amazonas by ten *Vanilla* and four *Epistephium* species, although research on the latter remains

scarce. Recent studies documented *V. sprucei* for Brazil and *V. labellopapillata* for Amazonas (Krahl et al., 2025b, 2020b), while *V. sprucei* was also shown to be distinct from *V. trigonocarpa* (Karremans et al., 2020); *Vanilla* species were also treated by Klein et al. (2019) and Krahl (2020).

Pansarin (2025) clarified the taxonomy of *V. palmarum* and *V. lindmaniana*, showing that Amazonian populations previously identified as *V. palmarum* correspond to *V. lindmaniana*. Karremans et al. (2020) also synonymized *V. cristagalli* and *V. cristato-callosa*, both described from Amazonas, under *V. marowynensis*.

Pogonieae comprises six species in Amazonas, three each of *Cleistes* and *Duckeella*. Although specific studies are lacking, Pansarin et al. (2008) provided phylogenetic information on Amazonian species, while Batista et al. (2023) clarified the *C. rosea* species complex.

CYPRIPEDIOIDEAE

The subfamily Cypripedioideae comprises five genera and about 170 species, mainly terrestrial “slipper orchids” distributed across Asia, Europe and the Americas (Chase, et al., 2015). In Brazil, it includes *Phragmipedium* Rolfe and *Selenipedium* Rchb.f., totaling 11 species (Pessoa, et al., 2025). Both genera occur in Amazonas, represented by *P. longifolium* and *S. palmifolium*, which differ by their conduplicate and plicate leaves, respectively (Pridgeon, et al., 1999).

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No specific study has focused on Cypripedioideae in Brazil (Pessoa, et al., 2025), although broader studies provide relevant information. Guo et al. (2012) investigated the evolutionary history and biogeography of slipper orchids, including *P. longifolium*, while Braem (2015, 2016) examined the *P. longifolium* complex. Sambin & Chiron (2019) also contributed to the taxonomy and morphology of the *S. palmifolium* complex in French Guiana.

ORCHIDOIDEAE

The subfamily Orchidoideae comprises about 3,600 species in 208 genera worldwide and 387 species in Brazil, including 35 in Amazonas (Chase, et al., 2015; Pessoa, et al., 2025). *Habenaria* Willd. is the most diverse genus in the state, with 21 species, and represents the tribe Orchideae and subtribe Habenariinae. Its species are relatively well studied through taxonomic revisions by Batista et al. (2006, 2008), the New World synopsis by Batista et al. (2011a, 2011b), and phylogenetic analyses by Batista et al. (2013).

Cranichideae comprises 14 species in three subtribes and nine genera, each represented by one species in Amazonas except *Sarcoglottis* C. Presl, with two species, one treated by Krahling (2020) and Krahling et al. (2021a). Specific taxonomic studies for these genera in Amazonas are lacking. Available information derives mainly from phylogenetic studies (e.g., Salazar, et al., 2003, 2018; Smidt, et al., 2021a) and broader taxonomic treatments, including *Prescottia* by Azevedo et al. (2014) and Goodyerinae by Engels & Smidt (2026). Engels & Smidt (2025) also contributed to the taxonomy and nomenclature of *Eltroplectris pauciflora*, originally described from material collected in Amazonas.

EPIDENDROIDEAE

The subfamily Epidendroideae comprises about 20,000 species in 576 genera, representing the most diverse Orchidaceae subfamily (Chase, et al., 2015). In Brazil, it includes 2,063 species (Pessoa, et al., 2025), of which 401 occur in Amazonas, distributed across 10 tribes, 16 subtribes and 93 genera, making it the largest Orchidaceae subfamily in the state. The tribes and subtribes are discussed separately below.

1. Tribe Cymbidieae

The Cymbidieae tribe comprises ten subtribes, nine occurring in Brazil and Amazonas (Chase, et al., 2015; Pessoa, et al., 2025). It is the most diverse tribe in Amazonas, with 215 species, particularly Catasetinae (54 spp.), Oncidiinae (52 spp.), Maxillariinae (46 spp.), Zygopetalinae (32 spp.) and Stanhopeinae (23 spp.), while Coeliopsidinae, Cyrtopodiinae, Eriopsidinae and Eulophiinae each have two species.

1.1. Catasetinae

The subtribe Catasetinae comprises eight genera, seven occurring in Brazil and five in Amazonas (Chase, et al., 2015; Pessoa, et al., 2025). *Catasetum* Rich. ex Kunth is the most diverse, with 38 species, including 15 endemic to Amazonas. Studies mainly address new species (Petini-Benelli, 2016; Valsko, et al., 2019; Krahling, et al., 2021c; Krahling, et al., 2023a, 2023b; Krahling, et al., 2024a), natural hybrids (Krahling, et al., 2020c; Krahling, et al., 2023c; Krahling, et al., 2025c, 2025d, 2025e), and new records (Krahling, et al., 2025a), complemented by Braga (1977a), Klein et al. (2019), and Krahling (2020).

Broader contributions include Silva & Silva (1998), while Mauad et al. (2022) provided a phylogenetic framework including several Amazonian species. Given the increasing number of taxa, comprehensive taxonomic treatment is needed. *Galeandra* Lindl., with three species in Amazonas, is comparatively well studied through Monteiro (2007) and Monteiro et al. (2009). Conversely, *Clowesia* Lindl., *Mormodes* Lindl. and especially *Cynoches* Lindl. require further studies, despite molecular phylogenies for *Mormodes* (Salazar, et al., 2016) and *Clowesia* (Tamayo-Cen, et al., 2022), the latter also treating the two *Clowesia* species occurring in Amazonas.

1.2. Oncidiinae

Currently, Oncidiinae comprises 63 genera, 38 occurring in Brazil and 19 in Amazonas (Chase, et al., 2015; Pessoa, et al., 2025). It is the second richest subtribe in the state, with *Notylia* Lindl. and *Rodriguezia* Ruiz & Pav. (7 spp. each) and *Trichocentrum* Poepp. & Endl. (5 spp.) being the most diverse.

Studies in Amazonas mainly report new national and state records, including *Quekettia vermeuleniana* (Valsko, et al., 2014a), *Notylia angustifolia* (Krahl, et al., 2015a) and *Plectrophora schmidtii* (Krahl, et al., 2021b), as well as the description of the interspecific hybrid *Ionopsis* × *atalibae* (Krahl et al., 2021d). Broader taxonomic studies provide additional information on *Lockhartia* (Blanco-Coto, 2011), *Macradenia* (Koch, 2016), *Notylia* (Oliveira, et al., 2026), *Rodriguezia* (Pessoa; Christenhusz, 2024) and *Trichocentrum* (Cetzal-Ix, et al., 2016).

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1.3. Maxillariinae

The generic circumscription of Maxillariinae has shifted from a genus-based approach (Blanco, et al., 2007) to broader clustering perspectives (Schuiteman, et al., 2015; Meneguzzo; Chase, 2024a). Brazil currently has seven genera, three occurring in Amazonas (Pessoa, et al., 2025): *Maxillaria* Ruiz & Pav. (39 spp.), *Bifrenaria* Lindl. (6 spp.) and *Xylobium* Lindl. (1 sp.).

No study has specifically addressed Maxillariinae in Amazonas; available information derives from broader taxonomic works, including Koehler & Amaral (2004) and Meneguzzo & Chase (2024a) for *Bifrenaria*, Koehler et al. (2012) and Schuiteman et al. (2015) for *Maxillaria*, and Ormerod (2018) for *Xylobium*.

1.4. Stanhopeinae

Of the 73 Stanhopeinae species recorded in Brazil (Pessoa, et al., 2025), 23 species in nine genera occur in Amazonas, with *Coryanthes* Hook. (10 spp.) and *Gongora* Ruiz & Pav. (5 spp.) being the most diverse.

Taxonomic studies in Amazonas have mainly focused on new species of *Coryanthes* and *Gongora*, including *C. dasilvae*, *C. elianae*, *C. erectiscapa*, *C. miuaensis* and *C. tefeensis* (Barros, 2001; Silva; Oliveira, 1998a; Chiron; Marçal, 2022; Chiron, et al., 2020), as well as *Gongora jauariensis* and *G. juruaensis* (Silva; Campacci, 2009, 2010). Broader taxonomic information on *Coryanthes* is provided by Chiron & Marçal (2021), including infrageneric organization and detailed distributions of the ten species occurring in Amazonas.

1.5. Zygopetalinae

The Zygopetalinae subtribe comprises 36 genera, 21 occurring in Brazil (Chase, et al., 2015; Pessoa, et al., 2025). In Amazonas, it includes 32 species in 10 genera, with *Dichaea* Lindl. being the most diverse (17 spp.; 53.1% of the subtribe).

Studies have focused mainly on *Dichaea*, including new species descriptions and taxonomic synonymizations and reaffirmations (Valsko, et al., 2014c; Krah, et al., 2015b, 2016b, 2024b). Information on other Zygopetalinae remains scarce and is largely restricted to broader taxonomic studies by Meneguzzo (2013), Hall (2015), Meneguzzo et al. (2015) and Meneguzzo (2020).

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1.6. Others Cymbidieae

The other Cymbidieae subtribes (Coeliopsidinae, Cyrtopodiinae, Eriopsidinae and Eulophiinae) are represented by only two species each in Amazonas and generally lack comprehensive state-level studies. In Eulophiinae, *Eulophia alta* and *Oeceoclades maculata* are considered naturalized in Brazil (Pessoa, et al., 2025).

Cyrtopodiinae species were treated by Romero-González et al. (2008), while *Eriopsis biloba* and *E. sprucei* were included in the revision of *Eriopsis* by Romero-González et al. (2015). Local treatments also include these subtribes (e.g., Klein, et al., 2019; Krah, 2020), including *Peristeria pendula* and *Eriopsis sprucei*, the latter treated as *E. sceptrum* by Klein et al. (2019).

2. Tribe Epidendreae

The Epidendreae tribe comprises six subtribes, five of which occur in Brazil (Chase, et al., 2015; Pessoa, et al., 2025). In Amazonas, it includes Laeliinae (81 spp.) and Pleurothallidinae (60 spp.), totaling 141 species and ranking as the second most diverse tribe after Cymbidieae.

2.1. Laeliinae

The Laeliinae subtribe comprises 81 species in 12 genera in Amazonas, making it the most diverse subtribe of Epidendreae in the state. *Epidendrum* L. is the richest genus (40 spp.), followed by *Encyclia* Hook. and *Scaphyglottis* Poepp. & Endl. (9 spp. each).

Studies in Amazonas mainly report new occurrences, including *Nidema ottonis* (Krahl, et al., 2014b), *Scaphyglottis punctulata* (Araújo, et al., 2022) and *Prosthechea jauana* (Vieira, et al., 2024). Broader taxonomic treatments include *Brassavola* R. Br. (Nogueira-Savelli, 2020), *Encyclia* Hook. (Bastos, et al., 2018), *Orleanesia* Barb. Rodr. (Gonçalves, et al., 2019) and *Prosthechea* Knowles & Westc. (Silva, 2021). Regional treatments by Braga (1977a), Klein et al. (2019) and Krahl (2020) also cover several Laeliinae species in Amazonas.

2.2. Pleurothallidinae

The Pleurothallidinae subtribe comprises 62 species in 18 genera in Amazonas, with *Octomeria* R. Br. (13 spp.), *Anathallis* Barb. Rodr. (10 spp.), *Acianthera* Scheidw. (7 spp.) and *Stelis* Sw. (6 spp.) being the most diverse. Studies have focused mainly on new records and species descriptions, including *Trichosalpinx egleri* (Krahl, et al., 2014a), *Muscarella aristata* (Pessoa, et al., 2013), and the rediscovery and first Brazilian record of *Octomeria romerorum* (Krahl, et al., 2022a).

New species and taxonomic additions include *Anathallis roseopapillosa* (Pessoa, et al., 2014), *A. amazonica* (Pessoa; Alves, 2015), *A. manausensis* (Krahl, et al., 2016a), *Dryadella osmariniana* (Braga, 1977b), and *Masdevallia britoi* (Pessoa; Karremans, 2022). Broader taxonomic treatments of *Dryadella* (Imig, et al., 2024), *Karma* (Karremans, 2023), *Lankesteriana* (Karremans, 2014) and *Octomeria* (Forster, 2007), together with regional treatments by Braga (1977a), Klein et al. (2019) and Krahl (2020), further contribute to understanding the diversity and distribution of Pleurothallidinae in Amazonas.

2.3. Others Epidendroideae

The tribes Gastrodieae, Malaxideae, Neottieae, Sobralieae, Triphoreae, Vandaeae, Wulschlaegelieae and Xerorchideae occur in Amazonas with relatively low species richness. Sobralieae is the most diverse, with 17 species in *Elleanthus* C. Presl (6 spp.) and *Sobralia* Ruiz & Pav. (11 spp.), although both genera remain poorly studied locally; available studies include Braga (1977a), Klein et al. (2019) and Krahll (2020), covering species such as *Sobralia bletiae*, *S. fragrans*, *S. granitica*, *S. macrophylla* and *S. sessilis*.

Vandaeae comprises 10 species, including eight *Campylocentrum* Benth. species in Angraecinae, whose taxonomy was revised by Pessoa & Alves (2016a, 2016b, 2018), and two *Polystachya* species addressed by Peraza-Flores et al. (2011). Local studies also include Braga (1977a), Klein et al. (2019) and Krahll (2020).

Malaxideae includes six species in *Bulbophyllum* Thouars, *Liparis* Rich. and *Malaxis* Sol. ex Sw. The group has been treated in comprehensive taxonomic studies, including Smidt (2007), Santos (2023) and Santos (2024), although specific studies in Amazonas are lacking.

Neottieae comprises six *Palmorchis* Barb. Rodr. species, which remain poorly studied in Amazonas. Available information derives mainly from taxonomic treatments by Szlachetko & Baranow (2014), Szlachetko et al. (2018), Damián-Parizaca & Montenegro (2018), Sambin et al. (2020) and Sambin & Aucourd (2024). Notably, Damián-Parizaca & Montenegro (2018) described *P. loretana*, with a paratype from the Adolpho Ducke Forest Reserve in Manaus.

Gastrodieae and Wulschlaegelieae are each represented by one mycoheterotrophic species, *Uleiorchis ulei* and *Wulschlaegelia calcarata*, whose taxonomy was addressed by Born et al. (1999); the latter was also included in Krahll (2020).

Finally, Triphoreae is represented by two terrestrial *Triphora* Nutt. species, which remain poorly known in Amazonas. Krahll (2020) provides the main local treatment, including *T. amazonica* in the floristic and taxonomic survey of the Adolpho Ducke Forest Reserve.

NATURAL HYBRIDS IN THE STATE OF AMAZONAS

Records of natural hybrids of Orchidaceae in Amazonas began in the 1970s with Pabst (1975), who described *Catasetum* $\times$ *issanense* and documented natural hybridization in *Catasetum* Rich. ex Kunth. Braga (1978) subsequently described $\times$ *Brassocattleya rubyi*, an intergeneric

hybrid, demonstrating that natural hybridization in the region extends beyond intrageneric crosses.

After a long gap, research resumed around 2020, with *Catasetum* × *louiseae* described by Krahling et al. (2020c) and *Ionopsis* × *atalibae* by Krahling et al. (2021d), expanding documentation to Oncidiinae. Subsequent studies described *Catasetum* × *grasineideae*, *C.* × *abreuanum*, *C.* × *angelae*, and *C.* × *humaitaense* from collections made in Amazonas (Krahling et al., 2023c, 2025c, 2025d, 2025e), highlighting natural hybridization as a recurring phenomenon, particularly in *Catasetum*.

More recently, Petini-Benelli (2025) reported *Catasetum* × *tapiriceps* in Amazonas through *Flora e Funga do Brasil*. Originally described from collections in the upper Orinoco River, Venezuela (Romero-González; Carnevali, 1989), this record expands the known distribution of the hybrid and reinforces the importance of continued research on Amazonian Orchidaceae.

OTHER RESEARCH AREAS ON ORCHIDACEAE IN AMAZONAS

1. Reproductive biology

In Amazonas, studies on the reproductive biology of Orchidaceae began with Braga (1976), who recorded *Eulaema mocsaryi* as a pollinator of *Stanhopea candida*, while *Euglossa ignita* acted as a “scent thief.” Braga (1977a) later compiled information on pollinators and pollination mechanisms for 33 Orchidaceae species from campina and campinarana around Manaus, although some records remained unknown.

After more than three decades, Jürgens et al. (2009) showed that *Eulophia alta* is exclusively melittophilous and is pollinated by 19 insect species, mainly bees. Storti et al. (2011) demonstrated that *Cattleya wallisii* is effectively pollinated by a single bee species, *Eulaema mocsaryi*.

Krahling (2013) reviewed information on four species previously studied by Braga (1977a), documenting new pollinators and differences from previous observations. *Encyclia mapuerae* was pollinated by females of *Centris varia*; *Maxillaria superflua* by *Trigona williana*; *Maxillaria lutescens* by *Melipona illustris* and *Trigona fulviventris*; and *Maxillaria prolifera* by *Polybia bistrata*. These findings were subsequently published by Krahling et al. (2015c, 2017, 2019, 2022d).

More recently, Krahling (2020) investigated *Prosthechea aemula* in campina/campinarana near Manaus and found that it is pollinated by males of *Euglossa*. This represents the most recent study devoted exclusively to Orchidaceae reproductive biology in Amazonas.

Other contributions include Krahll et al. (2012), who investigated the reproductive system of Amazonian species, and Krahll et al. (2014c), who studied the location of osmophores in *Epidendrum nocturnum*. Although more specific in scope, these studies have expanded knowledge of the reproductive mechanisms and ecological strategies of Amazonian Orchidaceae.

2. Anatomy

Studies on Orchidaceae anatomy in Amazonas are mainly based on historical research conducted at INPA, particularly by Luiz Carlos de Matos Bonates. His master's thesis focused on ecophysiological aspects of terrestrial Orchidaceae in the campina of the INPA Biological Reserve, relating photosynthetic pathways to environmental and leaf anatomical features (Bonates, 1987). This work led to subsequent studies identifying CAM and C₃ metabolism and highlighting leaf anatomy as an important component of ecological adaptation (Bonates & Braga, 1992).

Bonates (1993) further investigated the ecological anatomy of CAM orchids from the same campina, documenting features associated with water regulation and adaptation to oligotrophic and seasonally dry conditions, including succulence, leathery leaves, thickened cuticles, developed hypodermis, and chlorenchyma organization. This research was expanded in the author's doctoral thesis, which incorporated roots and leaves of epiphytic orchids and provided an integrated interpretation of structural and physiological adaptations to nutrient-poor and water-limited environments (Bonates, 2007). Together, these studies represent the main historical reference for Orchidaceae anatomy in Amazonas, particularly in campina ecosystems.

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3. Morphometry

Despite its relevance, morphometric studies of Amazonian Orchidaceae remain scarce, particularly in Amazonas, with most studies including only limited Amazonian sampling. Notable examples include Araújo et al. (2023), Camelo-Júnior et al. (2022) and Pessoa et al. (2020).

Araújo et al. (2023) analyzed 136 flowers from 12 *Scaphyglottis* species, including seven of the nine species recorded in Amazonas, demonstrating the usefulness of floral shape for taxon discrimination. Camelo-Júnior et al. (2022) analyzed the labellum of 278 flowers in the

Trichocentrum cepula complex, including *T. sprucei*, one of five species recorded in Amazonas, which showed distinct morphometric patterns from the other taxa. Pessoa et al. (2020) analyzed 144 flowers of the *Epidendrum difforme* complex and found morphological groups consistent with molecular and cytogenetic evidence. *Epidendrum althausenii*, one of 40 *Epidendrum* species recorded in Amazonas, was included in the overall sample but excluded from morphometric analyses because only two flowers were available, illustrating a common limitation for Amazonian taxa.

4. Ecology and conservation

In Amazonas, ecological information remains limited. Irume et al. (2013) recorded 164 epiphytic angiosperms in terra firme forest, while Boelter et al. (2014) found that soil nitrogen and phosphorus influence epiphytic community composition. Quaresma et al. (2017) reported distinct assemblages in floodplain and igapó forests, with greater richness in floodplains. In campinaranas, microsite availability strongly structures holoeiphytic communities (Marí et al., 2016), while Klein et al. (2022) recorded 112 species, including 66 Orchidaceae.

Few studies focus exclusively on orchids. Cruz & Braga (1997) documented host-tree selectivity, whereas Monteiro et al. (2022) recorded 17 orchid species in campinaranas near Manaus and highlighted threats from habitat loss.

FINAL CONSIDERATIONS

This review provides an updated overview of Orchidaceae in Amazonas, highlighting its high taxonomic richness and persistent knowledge gaps. The state harbors a significant proportion of Brazilian species, including endemic taxa associated with specialized environments such as campinas, campinaranas and seasonally flooded forests.

Research remains geographically and taxonomically uneven, with emphasis on Manaus and a few groups. Continued descriptions of new species, records and nomenclatural changes indicate that Orchidaceae diversity in Amazonas is still underestimated. Expanding research to herbarium specimens is therefore essential to improve knowledge of species composition, detect new taxa and geographic records, identify conservation priorities, and strengthen orchid collecting throughout the state.

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