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Sweet potato, morning glories, bindweeds: an overview of Convolvulaceae

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Abstract: Convolvulaceae are an economically and ecologically important plant family, including the crop sweet potato, ornamental morning glories, bindweeds and dodders. In the past 20 years, much progress has been made in the taxonomy and systematics of the family at several scales. The integration of molecular phylogenetics has revolutionised our understanding of the species and their relationships. Other fields such as ecology, evolution, phytochemistry, palynology, anatomy and genomics have also taken significant leaps. These new insights have levered a fast-paced progress that we are now experiencing, enhanced by the power of international collaborations. In this review, we summarise and reconcile the most meaningful advances in several fields that have impacted Convolvulaceae in recent years, pointing to the outstanding questions that will be the priority for the upcoming research in this plant family. Standardised guidelines for best practices in some techniques are also provided, such as field collection, photography and molecular techniques, drawing from the combined experience of researchers working on this family.

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1. What are Convolvulaceae? Diversity and characterisation

The Convolvulaceae currently comprises of 57 genera and 1,955 accepted species (POWO, 2024), classified into six subfamilies and 12 tribes (Table 1). The family is geographically widely distributed across temperate, tropical and subtropical regions. The greatest diversity is concentrated in the tropics and subtropics, with fewer representatives in temperate regions. Ecologically, a vast number of species show a preference for open or disturbed habitats, and, for this reason, are often mistaken for non-native, or invasive weeds; they rarely occupy dense primary forests. Members of Convolvulaceae most commonly present a climbing habit, either slender (e.g. *Convolvulus* L., *Jacquemontia* Choisy, *Xenostegia* D.F. Austin & Staples) or robust, woody vines (e.g. *Decalobanthus* Ooststr., *Dicranostyles* Benth., *Erycibe* Roxb., *Maripa* Aubl.) but they can also take the form of prostrate herbs (e.g. *Dichondra* J.R. Forst. & G. Forst., *Evolvulus* L.), subshrubs or shrubs (e.g. *Astripomoea* A. Meeuse, *Seddera* Hochst.), or rarely trees (*Humbertia madagascariensis* Lam., *Ipomoea arborescens* (Humb. & Bonpl. ex Willd.) G. Don) and holoparasitic climbers (*Cuscuta* L.).

Morphologically, species of Convolvulaceae can be recognised for their stems twining clockwise, without stipules or tendrils; alternate leaves, simple or compound, rarely fasciculate; calyx with a single whirl of five independent sepals, not fused (except in some species of *Cuscuta*); flowers with sympetalous (fused) corollas, bearing five conspicuous mid-petaline bands which can vary in colour or indumentum from the remainder of the corolla; five stamens adnate to the tube base or the corolla throat; superior ovary, bicarpellate, rarely tricarpellate, always with two ovules per carpel; fruit most commonly a dehiscent, four-seeded, dry, loculicidal or septicidal, capsule, less often carrying six or up to ten seeds; few members have berry (dry or fleshy) fruits (e.g. *Argyreia* Lour.) (Ooststroom & Hoogland, 1953; Austin & Cavalcante, 1982; Simão-Bianchini, 1991; Simão-Bianchini & Pirani, 1997; Staples, 2012; Silva *et al.*, 2018). A molecular synapomorphy of Convolvulaceae is the deletion of the *rpl*2 intron in the chloroplast genome (Stefanović *et al.*, 2003).

The most helpful characters for separating subfamilies within Convolvulaceae are the number and shape of styles and stigmas, except for subfamily Cuscutoideae, which carries great diversity in these characters (Table 2). This subfamily is, however, easily distinguished from the others for its parasitic life form, with yellow to orange stems, often presenting haustoria, very reduced or absent leaves, and minute flowers and fruits. It can often be confused with another parasitic plant, *Cassytha*, in family Lauraceae (Magnoliids), but easily distinguishable for the trimerous flowers (tepals) instead of five (petals and sepals) in *Cuscuta* (Silva *et al.*, 2021).

There are a few unique morphological characters that support the current tribe circumscription, but tribes are, instead, more often distinguished by a combination of morphological traits rather than a single feature. These rely, for example, on pollen characters (presence or absence of large spines, disposition and number of apertures), ovary, fruit or inflorescence morphology. At generic level, important taxonomic characters for distinction are: stigma shape; fruit dehiscence; corolla shape; corolla indumentum; ovary (number of loci, indumentum); pollen aperture number,disposition and exine ornamentation; bract shape; sepal shape; leaf venation pattern or division (i.e. entire vs compound); indumentum type (stellate, malpighiaceous, with or without glandular base, simple, bifid, etc.). At species level, key characters are sepal shape and size, corolla size or lobing pattern; leaf shape and lobing; habit.

Why study Convolvulaceae?

2.1 Economic importance and traditional uses

Convolvulaceae are an economically significant plant family, with a range of economic and traditional uses including ornamental, food, medicinal and recreational drugs. One of such key species is the crop sweet potato (*Ipomoea batatas* (L.) Lam.), a staple in the human diet, with a global trade value of USD 744 million as of 2022 (The Observatory of Economic Complexity, https://oec.world). Its high nutritional content, including essential vitamins, minerals, and dietary fibre, combined with its resilience to drought, makes it

Table 1. Diagnostic characters for subfamilies of Convolvulaceae.

Subfamily	Style	Stigma	Stigma shape
Cuscutoideae	1 or 2	2	Globose to ellipsoid
Humbertioideae	1	1	Capitate
Eryciboideae	0 (much compressed)	1	Disc (flattened)
Cardiochlamydeae	1	1	Globose
Dichondroideae*	2	2 or 4	Globose, club-shaped or filiform
Convolvuloideae	1	2	Globose, club-shaped or filiform

a crucial component for food security strategies, being an adaptable crop across a diversity of climates (Alam, 2021). Beyond its role as a staple food, sweet potato offers potential health benefits. It is a nutrient-dense, low-glycaemic option that supports balanced blood glucose levels. Sweet potatoes are also rich in anthocyanins, including peonidin and cyanidin derivatives, which exhibit antioxidant and anti-inflammatory properties, potentially surpassing other vegetables due to their free radical scavenging abilities. These compounds may help mitigate oxidative stress, a factor linked to chronic conditions such as cardiovascular disease and diabetes (Willcox *et al.*, 2009; Li *et al.*, 2019).

Other species in Convolvulaceae are known for their enlarged storage roots, which often serve as survival food during times of scarcity (e.g. *Ipomoea capillacea* (Kunth) G. Don; *I. jicama* Brandegee, from Tropical America, and *I. longituba* Hallier f. in East Africa) (Urbina, 1906; Kabuye, 1986; Sandoval-Ortega *et al.*, 2023). There are also some species in the Northeast of Brazil which roots are collected from the wild for human consumption: these are popularlyknown as "batata-da-serra" or "batatinha-da-serra", and despite the name ("batata" meaning "potato"), the taste is similar to pear. These species were found being marketed locally before they were recognised by science, i.e. *Ipomoea pintoi* O'Donell, *I. ana-mariae* L.V. Vasconcelos & Sim-Bianch., and *I. serrana* Sim-Bianch. & L.V. Vasconcelos, and they are rare, despite being explored as a food source (Vasconcelos *et al.*, 2016).

Another economically significant species in the family is *Ipomoea aquatica* Forssk., commonly grown as a vegetable for its edible leaves and stems, and particularly popular in Asia, known as 'water spinach (English), 'kankong' (Malay) or 'pak bung' (Thai). Its leaves are rich in dietary fibres and glycosides, which have also been associated with hypoglycaemic and antioxidant properties (Hamid *et al.*, 2011). *Ipomoea aquatica* has been utilised in southern Asia since at least A.D. 300, and possibly as early as 200 B.C. People have traditionally gathered this plant from the wild and cultivated it for its nutritional and medicinal value. When Europeans arrived in southern Asia during the late 1400s, they recognised its benefits and contributed to its dissemination worldwide (Austin, 2007).

Beyond dietary uses, Convolvulaceae include species with medicinal, cultural, and other practical applications. Medicinally, the roots of *Ipomoea purga* (Wender.) Hayne have been cultivated in Mexico for centuries for their purgative properties, forming part of a traditional production system that supports local economies (Urbina, 1906; Linajes *et al.*, 1994). *Ipomoea stans* Cav., also from Mexico, and commonly known as 'tumbavaqueros', has shown anxiolytic, sedative, and anticonvulsant properties, supporting its traditional use for nervous disorders and seizures (Díaz, 1976; Herrera-Ruíz *et al.*, 2007). Likewise, *Bonamia ferruginea* (Choisy) Hallier f. ('cipó-tuíra') is traditionally used in Brazil to treat jaundice, hepatitis, and malaria (Rodrigues, 2006; Paes & Mendonça, 2008). Furthermore, *Ipomoea mauritiana* Jacq. has been extensively investigated for its potential inclusion in herbal formulations due to its antihypertensive, fibrinolytic, and antioxidant activities (Chandira & Jayakar, 2010; Jain *et al*., 2011). *Ipomoea mauritiana* is often mis-cited in the literature as *Ipomoea digitata* (L.) L., a West Indian endemic that does not occur in Asia (Rhui-Sheng & Staples, 1995; POWO, 2024).

This family also includes plants with cultural significance, such as *Turbina corymbosa* (L.) Roth (syn. *Rivea corymbosa* (L.) Hallier f.), which has been used in ritual contexts by Mesoamerican civilisations and their descendants for its psychoactive effects, attributed to ergot alkaloids with similar effects to the psychedelic drug LSD [Lysergic acid diethylamide] (Schultes & Hofmann, 1973). The production of these compounds with hallucinogenic effects have been established to derive from a plant-fungal symbiosis, of which Convolvulaceae are a rare example among flowering plants (Panaccione *et al*., 2005; Schardl *et al*., 2007; Beaulieu *et al*., 2013; Florea *et al*., 2017; Steiner and Leistner, 2018; Cook *et al*., 2019; Olaranont *et al*., 2024). Additionally, *Ipomoea caudata* Fernald has been historically used in hunting, with its crushed roots employed as a fish poison to facilitate capture (Urbina, 1906).

Despite these known applications, many species within this family remain understudied, offering significant potential for future exploration. More detailed information on chemical compounds found in Convolvulaceae, their potential use and pharmaceutical properties can be found in the handbook "Solanaceae and Convolvulaceae: Secondary Metabolites:

Biosynthesis, Chemotaxonomy, Biological and Economic Significance (A Handbook)" (Eich, 2008). Examples of further uses can be found in Supplementary Materials (S6, S7). Convolvulaceae also have important ornamental value: with floral shapes ranging from funnel-form to bell-shaped and an impressive array of colours, many species are highly prized as ornamental plants. These species are celebrated globally, known as 'liserons' in French, 'morning glories' (*Ipomoea*) or 'bindweeds' (*Convolvulus* or *Calystegia* R.Br.) in English, 'campanillas' in Spanish, and 'asagao' in Japanese, of which *Ipomoea nil* (L.) Roth) and *I. indica* (Burm.) Merr. are among the most popular cultivated species. In Japan, the *asagao* hold a special place in culture, highlighted by the Iriya Asagao Matsuri, an annual festival in Tokyo that attracts morning glory fans, from July 6–8 (https://www.gotokyo.org/en/spot/ ev054/index.html). While many species are appreciated for their large, showy, flowers, others are appreciated for their decorative fruits (*Distimake tuberosus* (L.) A.R. Simões & Staples, or 'woodrose'), ornamental seeds (*Merremia discoidesperma* (Donn. Sm.) O'Donell, or "Mary beans"), or attractive foliage, such as *Dichondra repens* J.R. Forst. & G. Forst. Some species, like *Dinetus racemosus* (Roxb.) Sweet (syn. *Porana racemosa* Roxb.), are valued for their white-flowered, dripping, paniculate inflorescences, while compact shrubs like *Evolvulus nummularius* (L.) L. display charming small blue flowers covering the ground. These aesthetic qualities, coupled with their role in supporting pollinators, make Convolvulaceae essential in horticulture and in efforts to conserve biodiversity and promote ecological research.

2.2 Species richness and untapped diversity

With Convolvulaceae comprising 1,955 species, subfamily Convolvuloideae is, by far, the largest and most taxonomically diverse of all the six subfamilies, including 1,198 species (61% of the species of Convolvulaceae) and 24 genera (42% of the genera of the family); it is also the subfamily that includes some of the most economically important species, such as the crops "sweet potato" (*Ipomoea batatas* L.) and "water spinach" (*Ipomoea aquatica* Forssk.), the ornamental "morning glories" (*Ipomoea* spp.), and "bindweeds" (*Convolvulus* spp. and *Calystegia* spp.) (POWO, 2024, Table 1). At generic level, the species diversity is, also, very unevenly distributed. The greatest species richness is concentrated in three largest genera: *Ipomoea* (615 spp.), *Cuscuta* L. (220 spp.) and *Convolvulus* (203 spp.), which together contain 54% of the total number of species of the family. Other significantly diverse genera are *Argyreia* (143 spp.), *Jacquemontia* (106 spp.), *Evolvulus* (106 spp.), *Erycibe* (73 spp.) and *Bonamia* Thouars (70 spp.). Yet, more than half of the genera of Convolvulaceae (35 of the 57 genera) contain fewer than 10 species. Of these, a handful are likely to be soon submerged into other genera, for lack of phylogenetic support and morphological diagnosability, as was recently the case of *Blinkworthia* Choisy (Rattanakrajang *et al.*, 2018; Rattanakrajang *et al.*, 2022). However, many of these smaller, in some cases monotypic, genera represent distinct evolutionary lineages, morphologically clearly distinct and geographically restricted, such as the genera endemic to Madagascar (*Cardiochlamys* Oliv., *Humbertia* Lam., *Rapona* Baill.), Australia (*Duperreya* Gaudich, *Wilsonia* R. Br.) or Brazil (*Daustinia* Buril & A.R. Simões). Beside intrinsic biological and evolutionary reasons, it may also be that the most economically important genera (e.g. *Ipomoea*, *Convolvulus*) have historically received more attention and have, as consequence, seen more species described at a faster pace. Since 2000, 295 new species of Convolvulaceae have been described across 21 genera, of which 50% in *Ipomoea* alone, followed by *Cuscuta* (8%), *Convolvulus* (7%), *Jacquemontia* (7%), *Argyreia* (6%) and *Bonamia* (6%) (https://ipni.org, accessed Dec. 2024). More recent studies targeting smaller, less studied genera, such as *Evolvulus, Dicranostyles, Distimake, Erycibe, Maripa* or *Xenostegia* have demonstrated that there is still much undocumented diversity, with new species still being described (Silva *et al.*, 2014; Moreira *et al.*, 2021; Belo *et al.*, 2023; Santos *et al.*, 2023; Pastore *et al.*, 2023, 2024; Patil *et al.*, *in press*). More strikingly, in 36 of the 57 currently accepted genera of Convolvulaceae, not a single new species has been described in the past 24 years (since 2000). It is possible that the species-level diversity of the family has been significantly underestimated and could increase if more taxonomic studies were conducted on these overlooked genera, with targeted field collections and careful examination of herbarium collections.

2.3 Centres of diversity and endemism

Convolvulaceae are primarily found in tropical and subtropical regions, which house 52 of the 57 genera. The remaining five genera occur in temperate regions, of which two — *Calystegia* and *Polymeria* R.Br. — occur exclusively in temperate biomes (Mitchell *et al.*, 2016). *Convolvulus*, the largest genus in the tribe Convolvuleae, is widespread across temperate zones, exhibiting notable diversity in the Mediterranean, Western Asia, and the Southern Hemisphere temperate regions, such as southern Africa, Australasia, and South America (Wood *et al.*, 2015; Mitchell *et al.*, 2016). The Eastern Hemisphere (Paleotropics, or Old World) is an important centre of generic diversity for Convolvulaceae, hosting 77% of the family's generic richness (44 of the 57 genera), with 18 genera restricted to this region. The Western Hemisphere (primarily tropical Americas) houses 22 genera, half the diversity observed in the Eastern Hemisphere and fewer than the diversity of Madagascar alone, where 23 genera occur, including five endemic genera (Mitchell *et al.*, 2016). The African mainland supports 30 genera, of which nine are endemic, while Australasia and the Pacific contain 36 genera, with 11 regionally restricted. Similarly, tropical Asia and Malesia comprise 33 genera, including eight endemic genera, whereas Australia and Oceania harbour 19 genera, of which three are endemic (POWO, 2024).

Conservation

In general, the conservation status of the species of Convolvulaceae is poorly known: no more than 7% of all Convolvulaceae species have been red listed (IUCN, 2024). The genera with most species red listed are *Ipomoea* (*c.* 10% of the genus red listed, in a total of 65 species) of which 10% are CR, 20% are EN, 10% are VU, 3% are NT, 49% are LC, and 6% are DD (IUCN, 2024). Few studies have been carried out to assess the risk of extinction of Convolvulaceae species in the world, some with an approach to reforestation, as in Maschinski and Wright (2006) and Thornton *et al.* (2008), where both evaluated *Jacquemontia reclinata* House. Others focused on reproductive or genetic diversity and conservation of *Ipomoea microdactyla* Griseb. (Geiger *et al.*, 2012), and additionally, the diversity pattern and conservation implications under climate change scenarios for the island of Crete, have been analysed by Kougioumoutzis *et al.* (2020), and included two species of Convolvulaceae. Similarly, other studies have looked at the value of climate change in the prediction of geographic distribution in Convolvulaceae, and its potential impact on species' conservation, in the tropical Americas (Barbosa *et al.*, 2024; Brito *et al.* 2023).

In some works, the conservation assessments were done in the context of the local flora, although not submitted to the IUCN Red List, such as Fernández-Concha *et al.* (2021), who assessed the extinction risk of vascular plants endemic to the Yucatán Peninsula, including three species of Convolvulaceae; Syahida-Emiza *et al.* (2013), who assessed the conservation status of 17 species of the genus *Erycibe* for Peninsular Malaysia,;Alves and Buril (2022), for Espinhaço Range, Brazil, where they evaluated the areas of richness, endemism and diversity of Convolvulaceae in the region, but did not classify according to IUCN, and Moreira *et al.* (2018, 2019, 2021) in which they present new species of *Bonamia* for the Brazilian Cerrado, as well as the risk of extinction for each of them. In the Southeastern United States, 17 species of Convolvulaceae have been assessed as threatened (Radcliffe *et al.*, 2023). In Africa, four species of the family were found to be threatened, as included in the Red Data Book of the Flowering Plants of Cameroon (Onana *et al.*, 2011), three of which (*Neuropeltis* and *Calycobolus*) were incorporated into the IUCN Red List (https://iucnredlist.org, Accessed December 2024).

Notable endangered species of Convolvulaceae include *Evolvulus antillanus* Urb., a species native to the West Indies that is almost extinct in its natural habitat, likely due to cattle introduction, though it is preserved in botanical collections in Châtenay-Malabry and Brest (France). *Humbertia madagascariensis* Lam., a hardwood tree endemic to southeastern Madagascar, faces risk of extinction due to the loss of coastal rainforests. *Bonamia grandiflora* Choisy, endemic to Florida, suffers from habitat degradation and the suppression of natural fires, which impacts its competitiveness. Some species are only known from the type specimen (e.g., *Ipomoea pulcherrima* Van Ootstroom from Peru). Other rare species include *Turbina inopinata* Heine (New Caledonia), *Jacquemontia reclinata* (Florida), and *Bonamia menziesii* A.Gray (Hawai'i) (Landrein, 2012; Convolvulaceae Unlimited, https://convolvulaceae.myspecies.info).

Although many Convolvulaceae species are not considered high-priority conservation targets—and some are even managed for their invasive tendencies—such assumptions can overlook complex ecological challenges (Baucom, 2011; Fang *et al.*, 2013). For example, species adapted to disturbed habitats may face genetic bottlenecks or ecological vulnerabilities despite their apparent abundance (Kuester *et al.*, 2015, 2016; Williams-Linera *et al.*, 2021). The salt marsh morning glory (*Ipomoea sagittata* Poir.) exemplifies this complexity: although locally abundant, its low genetic diversity could render it highly susceptible to climate change and sea-level rise (Huerta-Ramos *et al.*, 2015).

Future conservation efforts for Convolvulaceae can benefit from existing regional and floristic studies, particularly for endemic and rare species. For this purpose, progress in integrating large datasets of ecological, geographic, and morphological evidence is necessary and remains slow, but the increased availability of digitised specimen collections facilitates the development of comprehensive geographic databases and will be powerful tools for advancing in this field. A concerted global initiative to consolidate such data and prioritise endangered species will be an important step to establishing effective conservation strategies for the family, e.g. building up on the existing Convolvulaceae Network and World Flora Online Taxonomic Expert Network working groups

Key advances in Convolvulaceae research

3.1 Systematics: the era of molecular phylogenetic analyses and the outstanding challenges

Convolvulaceae are classified in the order Solanales, as earlier proposed by traditional morphological classification systems (Cronquist, 1988; Dahlgren, 1989; Thorne, 1992) and reinstated by molecular-based classifications (APG IV, 2016; Zuntini *et al.,* 2024), being sister to Solanaceae (the family of nightshades, tomato, potato, eggplants), along with Montiniaceae, Sphenoclaeceae, and Hydroleaceae. The order Solanales belongs in the supra-order Lamiids, which also encompasses Lamiales and Boraginales (APG IV, 2016). Convolvulaceae can be distinguished from other families in the Solanales by the presence of laticifers, intraxylary phloem (likely shared with Solanaceae), common presence of successive cambia, and a set of unique seed and pollen morphological traits (Stevens, 2001). Takhtajan (1997) proposed the recognition of Convolvulaceae as a separate order, Convolvulales, based on these characters. It is the only family in the Asterid clade where seeds show physical dormancy (Jayasuryia *et al.,* 2008, 2009; Gunadasa *et al.,* 2024). Convolvulaceae also produce diverse critical secondary metabolites such as tropane alkaloids, and this trait is shared with its sister family Solanaceae (Eich, 2008). Despite several morphological coherence within Convolvulaceae, some authors have disputed this, and recognised new families such as Cuscutaceae, Dichondraceae, and Humbertiaceae from Convolvulaceae (Austin, 1973), thus splitting the family. The introduction of molecular phylogenetic analyses has come to demonstrate that Convolvulaceae is monophyletic, with the inclusion of *Cuscuta, Dichondra* and *Humbertia*, and therefore these genera should not be recognised as segregate families (Stefanović *et al.*, 2002, 2003; Simões *et al.*, 2022; Zuntini *et al.*, 2024).

Within Convolvulaceae, classification at subfamily and tribal level has also varied significantly between authors and over time, depending on the hierarchical value of the characters chosen to differentiate these higher-level divisions, for example: fruit type, ovary characters, style and stigma shape and number, etc. The first proposal of a supra-generic classification within Convolvulaceae was made by Choisy (1834), who created four "sections": Argyreieae - characterised by a syncarpous gynoecium and indehiscent fruits; Convolvuleae - characterised by a syncarpous gynoecium and dehiscent fruits; Dichondreae – presence of an apocarpous gynoecium and dehiscent fruits, and finally Cuscuteae - characterised by their parasitic life form. Later, Choisy (1845) re-ranked these "sections" as tribes, while retaining the names and the circumscription.

Another classification was later proposed by Hallier (1893), dividing the family into two 'subfamilies' based on the morphology of pollen grains: 1) Echinoconieae (including two tribes), characterised by pollen grains with echinate (spiny) exine, and 2) Psiloconieae (including seven tribes), characterised by pollen grains with psilate (non-spiny) exine. Later, Van Ooststroom (1953), classified Convolvulaceae into the subfamilies Cuscutoideae (composed solely of the tribe Cuscuteae), and Convolvuloideae (which included the tribes Convolvuleae and Ipomoeeae). The first phylogenetic analyses were introduced by Austin (1973, 1988), who proposed a cladogram based on morphological and cytological characters. From this phylogenetic proposal, he recognised nine tribes: Argyreieae, Ipomoeeae, Convolvuleae, Cuscuteae, Erycibeae, Hidebrandtieae, Cresseae, Poranae, and Dichondreae, as well as the doubtful group that he coined as 'Merremioids' (Austin, 1982).

The incorporation of molecular data into phylogenetic studies (Stefanovic *et al.*, 2002, 2003) has come to help settle the subfamily and tribal level classifications and has shown the systematic value of stigma and style characters, as synapomorphies at this taxonomic level (Table 1). For example, the division of Hallier (1893) based on pollen characters was proved consistent with the molecularphylogenetic results, with Echinoconieae resolved as monophyletic. Therefore, while molecular evidence has come to re-shape the higher-level classification of the family, it has also confirmed the systematic value of micromorphological characters used in past classifications, namely style, stigma and pollen, and reinforced their predictive value for systematic relationships.

Molecular phylogenetic studies have also offered greater clarity in tribal circumscription, confirming that some of the previously defined tribes were monophyletic, e.g. Convolvuleaee and Cuscuteae, while others needed to be re-circumscribed or needed further investigation, e.g. Cresseae, Poraneae or the "problematic" Merremieae (Stefanović *et al.*, 2002, 2003). An integrative approach has been taken to re- evaluate the circumscription of tribe Merremieae and its genera, resulting in an improved classification with monophyletic genera, morphologically and micromorphologically diagnosable genera, while the tribe itself was demonstrated to be polyphyletic, non morphologically diagnosable, and was dissolved (Simões *et al.*, 2015; Simões & Staples, 2017). The ambiguous generic placement of particular species has also been clarified by a combination of molecular and micromorphological evidence (Tamboli *et al.*, 2021; Pisuttimarn *et al.*, 2023). More recently, nuclear genomic data (Simões *et al.*, 2022; Zuntini *et al.*, 2024) has been helpful to resolve uncertainties in tribal delimitation and generic placement, for example suggesting for the first time a close relationship of genus *Distimake* with tribe Ipomoeeae, in a completely new relationship never hypothesised in previous studies, but otherwise confirming most of the known subfamily and tribal delimitations. At present, the circumscription of tribes Cresseae and Poraneae remain the least well established, and the position of the genera *Cuscuta* and *Erycibe* within the family is yet unresolved (Simões *et al.*, 2022). The dissolution of tribe Merremieae has also left nine genera unclassified at tribal level, and treated as "*incertae sedis*", pending further studies.

In general, the higher-level relationships within Convolvulaceae are among the biggest challenges yet to be overcome in this plant family. Even though most of the circumscriptions of subfamilies and tribes are stable in the most part, the uncertainty of the position of key genera such as *Cuscuta* and *Erycibe*, the uncertain classification of some of the "Merremioids", and the lack of support in the relationships between tribes themselves, means that a full re-classification of the family is not yet possible. This lack of a "phylogenetic backbone" also hinders broader scale evolutionary and biogeographic analyses.

The ongoing work is an integrative taxonomic approach by combining molecular phylogenetic tools with morphological data towards an improved subfamily and tribal level classification of the family. However, this effort is hindered mostly by incomplete sampling or the need of morphological data from a wide geographic region, as many of the genera and tribes span across different continents. An international collaborative effort is being coordinated to not only extensively sample DNA from all the Convolvulaceae genera across different biogeographic regions, but also to extensively morphologically, micromorphologically, geographically and ecologically characterise them, so that significant progress can be made in this sense.

3.2. Large genera vs diagnosable genera? A turning point for generic re-classification

The era of molecular phylogenetics has helped to successfully re-assess the circumscription of subfamilies and tribes and re-interpret the systematic value of traditionally used morphological and micromorphological characters. This is also true for traditionally recognised genera, especially the most

Table 2. Summary of Convolvulaceae Classification (based on Stefanović *et al.*, 2002; POWO, 2024).

Rank	Name	Species	Distribution
Subfamily	**CUSCUTOIDEAE**	**220**	**Temperate, Tropics & Subtropics**
Tribe	**Cuscuteae**	**220**	**Temperate, Tropics & Subtropics**
Genera	*Cuscuta*	220	Temperate, Tropics & Subtropics
Subfamily	**HUMBERTIOIDEAE**	**1**	**Madagascar**
Tribe	**Humbertieae**	**1**	**Madagascar**
Genera	*Humbertia*	1	Madagascar
Subfamily	**ERYCIBOIDEAE**	**73**	**Asia, Australia**
Tribe	**Erycibeae**	**73**	**Asia, Australia**
Genera	*Erycibe*	73	Asia, Australia
Subfamily	**CARDIOCHLAMYDEAE**	**24**	**Asia, Australia, Madagascar, C. America**
Tribe	**Cardiochlamyeae**	**12**	**Asia, Madagascar**
Genera	*Cardiochlamys*	2	Madagascar
	Cordisepalum	2	Asia
	Dinetus	8	Asia
Tribe	**Poraneae**	**12**	**Asia, Australia, Madagascar, C. America**
Genera	*Duperreya*	3	Australia
	Poranopsis	3	Asia, Australia, Madagascar, Central America
	Tridynamia	4	Asia
	Porana	2	Asia, Mexico
Subfamily	**DICHONDROIDEAE***	**439**	**Temperate, Tropics & Subtropics**
Tribe	**Cresseae**	**249**	**Temperate, Tropics & Subtropics**
Genera	*Bonamia*	70	Tropics
	Cladostigma	3	NE. & E. Tropical Africa, SW. Arabian Peninsula
	Cressa	5	Temperate & Subtropics
	Evolvulus	106	Tropics & Subtropics
	Hildebrandtia	11	NE. & E. Tropical Africa, Arabian Peninsula, Madagascar
	Itzaea	1	S. Mexico to Central America
	Neuropeltis	14	West & Central Africa, Asia
	Neuropeltopsis	1	Borneo
	Seddera	28	Africa, Arabian Peninsula, India
	Stylisma	7	Central & East USA

Rank	Name	Species	Distribution
	Wilsonia	3	Australia
Tribe	**Dichondreae**	**47**	**Africa, Tropical & Subtropical America, Australia, Madagascar**
Genera	*Calycobolus*	18	South Tropical America, West & Central Africa
	Dichondra	15	W. & S. U.S.A. to Tropical & Subtropical America, Mascarenes, Australia, New Zealand
	Dipteropeltis	2	West & Central Africa
	Falkia	3	Arabian Peninsula, Eritrea to S. Africa
	Metaporana	6	E. Central & E. Tropical Africa, Socotra, Madagascar
	Nephrophyllum	1	NE. Tropical Africa
	Petrogenia	1	Texas to NE. Mexico
	Rapona	1	Madagascar
Tribe	**Jacquemontieae**	**106**	**Tropics & Subtropics**
Genera	*Jacquemontia*	106	Tropics & Subtropics
Tribe	**Maripeae**	**37**	Central & S. Tropical America
Genera	*Dicranostyles*	16	Central & S. Tropical America
	Lysiostyles	1	N. South America to N. Brazil
	Maripa	20	SE. Mexico to S. Tropical America
Subfamily	**CONVOLVULOIDEAE**	**1,198**	**Temperate, Tropics & Subtropics**
Tribe	**Convolvuleae**	**240**	**Temperate & Subtropics**
Genera	*Convolvulus*	203	Temperate & Subtropics
	Calystegia	26	Temperate & Subtropics
	Polymeria	11	Lesser Sunda Islands to Australia, New Caledonia
Tribe	**Aniseieae**	**6**	**Tropical & Subtropical America**
Genera	*Aniseia*	3	Tropical & Subtropical America
	Odonellia	2	Mexico to South Tropical America
	Tetralocularia	1	South Tropical America
Tribe	**incertae sedis / "Merremieae"**	**137**	
	Merremia s.s.	10	Asia, Australia
	Merremia s.l.	34	Africa, Asia
	Distimake	46	Tropics & Subtropics
	Decalobanthus	19	E. Africa, Madagascar, Tropical Asia to Pacific

Rank	Name	Species	Distribution
	Hewittia	1	Tropical Africa and Tropical Asia
	Hyalocystis	2	NE. Tropical Africa
	Xenostegia	6	Tropical Africa, Tropical Asia & Australia
	Remirema	1	Thailand
	Operculina	13	Tropical America, Africa, Asia, Australia & Pacific
	Camonea	4	Tropics & Subtropics
	Daustinia	1	Brazil
Tribe	**Ipomoeeae**	**815**	**Tropics & Subtropics**
	Argyreia	143	Madagascar, Tropical Asia
	Astripomoea	12	Tropical & S. Africa, Arabian Peninsula
	Ipomoea	635	Tropics & Subtropics
	Lepistemon	7	Tropical Africa, Tropical & Subtropical Asia to NE. Australia
	Lepistemonopsis	1	NE. & E. Tropical Africa
	Paralepistemon	2	S. DR Congo to KwaZulu-Natal
	Rivea	3	S. & SE. Asia
	Stictocardia	13	Tropical Africa, Tropical Asia & Pacific
	Turbina	20	Central and South America, South Africa

*The name "Dichondroideae" is here applied to refer to the clade Dicranostyloideae ("bifid clade"), which has been lacking a formal recognition as subfamily since the phylogenetic revision of the classification of the family (Stefanović *et al.*, 2002; Stefanović & Olmstead, 2003). A new revision of the classification of the family is ongoing which may revisit the nomenclature of the subfamiliar and tribal divisions currently recognised.

species-rich, which have been under the spotlight of the new molecular approaches. While some genera have been confirmed to be monophyletic, such as *Convolvulus* (with the integration of *Calystegia*), *Evolvulus* or *Operculina*, others were resolved as non-monophyletic, opening a new path of investigation for generic re-classification, for example for *Ipomoea* (Wilkin, 1999; Manos *et al.*, 2001; Eserman *et al.*, 2014; Muñoz-Rodríguez *et al.*, 2019; Simões *et al.*, 2022), *Merremia* s.l. (Stefanović *et al.*, 2002; Simões *et al.*, 2015), *Seddera* (Stefanović *et al.*, 2002; Luna *et al.*, 2013) and *Bonamia* (Stefanović *et al.*, 2002; Simões *et al.*, 2022).

Genera like *Evolvulus*, *Hildebrandtia*, *Seddera*, and *Cladostigma* have all been subjects of monographic treatments in earlier decades, but these studies predate the molecular phylogenetic approaches now available, such as *Evolvulus* (Van Ooststroom, 1934), *Hildebrandtia* Vatke (Demissew, 1996), *Seddera* (Demissew & Mill, 2009) and *Cladostigma* Radlk. (Demissew, 1996). For example, while *Evolvulus* was initially defined based on corolla shape and fruit dehiscence, recent studies suggest that molecular data may redefine its taxonomic boundaries, especially in relation to closely related genera within the tribe. Similarly, *Hildebrandtia* and *Seddera* require molecular evidence to resolve their evolutionary relationships fully, especially considering recent studies that highlight polyphyletic lineages within the family (Luna *et al.* 2012).

Recent advances in molecular systematics have highlighted the need to reclassify polyphyletic genera within Convolvulaceae, such as *Ipomoea* and B*onamia*, which could significantly alter the number of recognised genera, particularly in the Eastern Hemisphere (Stefanović *et al.*, 2003; Mitchell *et al.*, 2016). For instance, the re-circumscription of the historically pantropical and polyphyletic genus *Merremia* s.l. has led to its division into four paleotropical genera — *Merremia* s.s., *Camonea, Decalobanthus,* and *Xenostegia* and one primarily neotropical genus, *Distimake,* which also includes substantial diversity in the Paleotropics (Mitchell *et al.*, 2016; Simões & Staples, 2017). Advances in molecular phylogenetics continue to provide critical insights that reinterpret morphological data, enabling more precise circumscription of genera and, as a general trend, an increase in generic richness, particularly in the Eastern Hemisphere (Williams *et al.*, 2014).

Other integrative monographs include that of *Convolvulus* (Wood *et al.,* 2015) and *Operculina* Silva Manso (Staples *et al.,* 2020). In addition to monographs, partial studies that either do not include molecular phylogenetic evidence, such as a synoptic revision of *Decalobanthus* Ooststr., (Staples, 2022), or focus only on a regional sub-section of the species of the genus, such as the African *Neuropeltis* Wall. (Breteler, 2010), the African *Calycobolus* Wild. ex Schult. (Breteler, 2013), the American *Merremia* (O'Donell, 1941) or the South American *Ipomoea* (Wood *et al.*, 2020).

Generic monographs is an area where much work is still necessary in Convolvulaceae, as there are many gaps that still need to be filled in across the family, but, in many groups, this is pending taxonomic revision at tribal level, to help elucidate generic circumscription in the light of new molecular phylogenetic data, as many of the currently recognised genera are yet polyphyletic and needing to be re-circumscribed. Nonetheless, significant taxonomic progress continues to occur at species level, with many new species recently described, namely in *Argyreia, Bonamia, Cuscuta, Distimake* or *Ipomoea* (Lawand & Shimpale, 2021), as well as new combinations, e.g. in *Distimake* (Petrongari *et al.,* 2018) or *Decalobanthus* (Simões *et al.,* 2020) or large scale nomenclature reviews, e.g. in *Argyreia* (Staples & Traiperm, 2017). Thus, meanwhile, a lot of detailed species information is available also in floristic treatments (Table 3; Supplementary Material S1) and other geographically oriented publications, e.g. South American *Ipomoea* (Wood *et al.,* 2020), *Ipomoea* from Ghana (Williams *et al.,* 2024) Convolvulaceae from Guinea (Davis *et al.,* 2024) or Convolvulaceae from Serra da Canastra (Kojima *et al.,* 2024), which are a good source of detailed, species-level information, for future revisionary studies.

One of the most challenging classification within Convolvulaceae is in the genus *Ipomoea*, the most species-rich genus in the family, encompassing 615 species (635 fide POWO, 2024; updated to 615 fide Simões *et al.*, 2024). Phylogenetic studies have shown that *Ipomoea* is not monophyletic and that nine genera are nested within it (Wilkin *et al.,* 1999; Manos *et al.,* 2001; Eserman *et al.,* 2014; Muñoz-Rodríguez *et al.,* 2019; Simões *et al.,* 2022). Furthermore, few of the proposed infrageneric subdivisions of *Ipomoea* are monophyletic when assessed with molecular data (Miller *et al.,* 1999; Manos *et al.,* 2001; Stefanović *et al.,* 2003). The reclassification of this large, widespread, incredibly variable genus remains a challenge, and efforts are ongoing to untangle it. A nomenclatural impediment to a re-classification of the group has recently been overcome (Eserman *et al.,* 2020; Applequist, 2023; Eserman *et al.,* 2023; Wilson, 2024). Before the acceptance of this nomenclatural proposal, numerous name changes of many species would have been required if the large genus *Ipomoea* had been split into smaller genera, potentially destabilizing the nomenclature of Neotropical taxa. Now, it is possible to preserve the names of economically important species like sweet potato, as well as to maintain the important generic names such as *Argyreia* and *Stictocardia*, with far less nomenclatural disruptions for both

Neotropical and Palaeotropical taxa (Simões et al. 2024).

One of the first major steps in the reclassification of the genus is the need for infrageneric monograph that clarify relationships and morphology across the genus. The most recent subgeneric classification proposed three subgenera: subgenus *Eriospermum*, subg. *Ipomoea*, and subg. *Quamoclit* (Austin & Huáman, 1996), but none of these subgenera correspond to monophyletic lineages, highlighting the complex morphological diversity in this group. The relatively small *Ipomoea* subgenus *Quamoclit* (ca. 85 species) has received the greatest number of taxonomic treatments (e.g. O'Donell, 1959; Gunn, 1972; McDonald, 1987, 1995, 2001; Eserman, 2012). However, the rest of the infrageneric groups comprising ca. 550 species of *Ipomoea* have not yet been treated nor re-assessed in the light of molecular phylogenetic reconstruction and detailed assessments of morphology.

The reason for this vast difference between morphologically based taxonomy and evolutionary relationships reconstructed using molecular data is the rapid and convergent evolution of many morphological traits commonly used to circumscribe species and infrageneric groups. For example, a three-locular ovary is a commonly accepted synapomorphy of *Ipomoea* series *Pharbitis*; however, another unrelated group, the newly described genus *Muigaia*, also has a three-locularcapsule, despite other syanpomorphies unique across tribe Ipomoeeae, such as quadrangular stems, deeply dissected leaves and leaf-like stipules at the petiole insertion (Ngima *et al., in press*). Furthermore, *Pharbitis* has also been described as having foliose sepals; this has also led taxonomists astray, leading some to interpret that some species of *Distimake* (Meissner, 1869) or even *Ipomoea pes-tigridis* (Hallier, 1893), completely unrelated taxa, to be closely related to *Pharbitis*.

The fact that most infrageneric classifications and taxonomic treatments of *Ipomoea* have been geographically biased (e.g. focusing on tropical Americas, East Africa or Malesia) has created great confusion, especially given the broad geographical range and morphological variation of this genus, and render most of these classifications irrelevant until they can be carefully tested against integrated phylogenetic studies (Austin & Huáman, 1996; Van Ooststroom 1953; Verdcourt 1963). As the availability of molecular data for tribe Ipomoeeae has seen exceptional progress in recent years (Wilkin et al., 1999; Manos et al., 2001; Eserman et al., 2014; Muñoz-Rodríguez et al., 2019; Simões et al., 2022), albeit with unbalanced sampling gaps for taxa from the Eastern Hemisphere which still needs to be overcome in the upcoming years, we are just starting to get a glimpse of the species-level relationships at a broader scale to be able to refine the boundaries of a monophyletic and morphologically diagnosable *Ipomoea* and establish, for the first time, a trans-geographic infrageneric classification for the genus, hand-in-hand with a comprehensive generic reclassification of the tribe Ipomoeeae. We are, after decades, or even centuries, of uncertainty and geographic biases, finally building up the necessary tools, global data, and a network of worldwide experts that could soon deliver a complete and global reclassification of this group at all scales: a sizeable challenge for the next years of taxonomic and systematic research in Convolvulaceae, both daunting and very exciting.

In the future, low coverage whole genome sequencing can be a promising approach to obtaining hundreds of genes, across all three genomes, for phylogenomic reconstruction. Genome sizes in *Ipomoea* are relatively small (2C = 1.5 to 5.2 pg) (Ozias-Akins & Jarret, 1994), and with the recent release of the Illumina NovaSeq X, it is now more accessible and affordable than ever to sequence genomes at low coverage.

3.3. Ecology and Evolution

The reproductive biology and pollination ecology have been major areas of research in the ecology of the Convolvulaceae, particularly focused within the genus *Ipomoea* (Baucom *et al.,* 2011). Evolutionary transitions from outcrossing to selfing in *Ipomoea*

Table 3. Progress on Flora treatments for the family Convolvulaceae, organized by region or country.

Continent	Region/Country	Year	Genera	Species
Africa	Convolvulaceae of Guinea	2024	16	51
America	Synopsis of the family Convolvulaceae in Mexico	2023	20	313
Oceania	Flora of New Zealand	2023	7	29
Americas	Flora of North America	2023	18	167
Asia	Flora of Mongolia	2022	4	15
Africa	Flora of Central Africa	2022	23	132
Americas	Flora de Veracruz III	2021	1	10
Americas	Flora do Brasil Online	2020	24	426
Americas	Catalogue of the Vascular Plants of Chile	2018	7	36
Asia	Flora of Cambodia, Laos and Vietnam	2018	22	108
Americas	Vascular Plants of Cuba	2017	12	95
Africa	Flore du Gabon	2015	9	31
Asia	Flora of Peninsular Malaysia	2015	16	79
Americas	Catalogue of the Vascular Plants of Bolivia	2014	17	186
Americas	*Convolvulaceae* of Sonora, Mexico II	2012	1	21
Americas	*Convolvulaceae* of Sonora, Mexico I	2012	9	84
Americas	Flora of the West Indies	2012	15	144
Asia	Co's Digital Flora of the Philippines	2011	17	75
Asia	Flora of Thailand	2010	24	119
Americas	Manual de plantas de Costa Rica	2010	17	75
Americas	Flora del bajío y regiones adyacentes II	2008	9	37
Americas	Flora del bajío y regiones adyacentes I	2007	1	50
Africa	Flora of Somalia	2006	18	58
Americas	Flora Fanerogámica del Valle de México	2005	5	34
Americas	Vines and Climbing Plants of Puerto Rico and the Virgin Islands	2005	11	45
Africa	Flora of Southern Africa	2000	16	114
Africa	Flora of Madagascar	2001	22	91
Americas	Catalogue of the Vascular Plants of Ecuador	1999	19	152
Asia	Flora of Taiwan	1998	14	44
Asia	Flora of China	1995	20	129

Continent	Region/Country	Year	Genera	Species
Americas	Flora de Veracruz II	1994	1	55
Americas	Flora de Veracruz I	1993	11	85
Americas	Catalogue of the Flowering Plants and Gymnosperms of Peru	1993	18	273
Oceania	Manual of the Flowering Plants of Hawai'i	1990	13	32
Americas	Flora of Panama	1987	14	158
Oceania	Flore de la Nouvelle Calédonie	1984	7	13
Oceania	Flora of Micronesia	1977	8	33
Asia	A dictionary of Flowering Plants in India	1973	20	180
Americas	Flora of Guatemala	1970	14	126
Asia	Flora of the U.S.S.R	1969	5	64
Africa	Flora of Tropical East Africa	1963	21	170
Asia	Flora Malesiana	1953	21	198
Africa	Flora of West Tropical Africa	1952	16	78
Americas	Convolvuloideas de Uruguay	1959	7	26
Americas	Convolvulaceas Argentinas	1959	12	86

have been associated with independent reductions in floral traits, including corolla size, nectar and pollen production, herkogamy (the spatial separation of anthers and stigma), and other characteristics collectively known as the "selfing syndrome" (Sicard & Lenhard, 2011; Rosas-Guerrero *et al.*, 2011; Rifkin *et al.*, 2019; Liao *et al.*, 2022). Such shifts increase reproductive assurance in environments with limited pollinator availability, but they are balanced by the potential negative consequences of inbreeding depression, which influences the diverse mating systems found in *Ipomoea* (Stucky, 1985; Díaz *et al.*, 1996; Kowyama *et al.*, 2000; Kaur *et al.*, 2018; Delgado- Dávila & Martén-Rodríguez, 2021).

Pollination studies on *Ipomoea* have predominantly emerged from North and Central America, where a wide array of pollinators including bees, butterflies, moths, and hummingbirds has been identified (Bullock *et al.*, 1987; Delgado-Dávila *et al.*, 2016; De Santiago *et al.*, 2019; Hassa *et al.*, 2020). The varying contributions of these floral visitors to reproductive success of *Ipomoea* highlight the importance of assessing pollinator effectiveness in ecological studies of plant-pollinator interactions (Araujo *et al.*, 2018; De Santiago *et al.*, 2019). The synchronisation of floral ephemerality, whether diurnal or nocturnal, plays a crucial role in shaping the temporal behaviour patterns of pollinators. (Gimenes *et al.*, 2021). Specifically, *Ipomoea* and *Jacquemontia* species are primarily visited by bees from the tribe Emphorini, which are solitary and oligolectic bees, collecting pollen from a restricted number of plant families, such as Convolvulaceae (Zanella, 2000; Pick & Schlindwein, 2011; Paz & Pigozzo, 2012, 2013; Paz *et al.*, 2013; Santos *et al.*, 2016; Paz *et al.*, *in prep.*), Cucurbitaceae (Silveira *et al.*, 2002), and Malvaceae (Schlindwein & Martins, 2000; Schlindwein, 2004). These records suggest a closer relationship between these bees and the species within these families, indicating that the pollen flow facilitated by phylogenetically related bees, along with high floral fidelity, may promote behaviours that enhance pollination efficiency (De Santiago *et al.,* 2019).

In addition to serving as foraging sources, the flowers of *Ipomoea* also act as sites for copulation and resting for the males of this tribe of bees, suggesting that they are essential for the maintenance of these pollinators in the region (Paz *et al.,* 2013; Gomes *et al.,* 2024). Despite extensive floral diversification aimed at attracting different pollinators, weak reproductive barriers have been found to permit the formation of fertile hybrids, highlighting the need for further research to clarify the roles of prezygotic and postzygotic isolation in speciation within the Convolvulaceae (Stucky, 1985; Díaz *et al.,* 1996; Babiychuk *et al.,* 2019). One mechanism identified as a potential benefit for selfing involves the close clustering of anthers around the stigma in some species, which not only facilitates high selfing rates but also protects against hybridisation through mechanical interference (Ennos, 1981; Smith & Rausher, 2007; 2008a, b). The speciose parasitic genus *Cuscuta* presents a unique example of regressive evolution where the host-parasite flowering synchronisation in *C. australis* is observed. Here, the parasite detects the FLOWERING LOCUS T (FT) protein expressed by the host and optimises its flowering time by synchronisation of its physiology with that of the host (Shen *et al.,* 2020). While *Cuscuta* consists of ~200 species, circumscribed into four subgenera, *C.* subg. *Cuscuta,* subg. *Grammica,* subg. *Monogynella,* subg. *Pachystigma*), their reproductive biology and need for the maintenance of flowers or sexual reproduction has rarely been studied. This further illustrates that flowering phenology and reproductive fitness mechanisms remains understudied in this family.

Convolvulaceae serve as an ideal model for studying mechanisms underlying floral trait evolution, particularly due to its numerous transitions in pollination syndromes that result in convergent flower colours and morphology, although key traits like floral scent composition remain understudied (Streisfeld & Rausher, 2009; Des Marais & Rausher, 2010). While *Ipomoea* remains the most extensively studied genus in pollination ecology, research on other genera such as *Calystegia*, *Argyreia*, *Operculina*, *Camonea* Raf., *Evolvulus*, *Hewitti*a Wight & Arn., and *Merremia* has revealed both the ecological diversity of the family and significant gaps in the current literature, especially in regions like Africa, Asia and Australia (Ushimaru & Kikuzawa, 1999; McMullen, 2009; Jirabanjongjit *et al.,* 2021; Paul *et al.,* 2023).

Ecological interactions related to seed dispersal among Convolvulaceae remain relatively unexplored, although effective dispersal strategies not only influence the colonisation of new habitats but also affect plant-pollinator interactions and the formation of complex plant communities. Morphological adaptations, such as the presence of lightweight and hairy seeds, favour dispersal by wind and water in various species of *Ipomoea* (Lakshminarayana *et al.,* 2022), as seen in the transoceanic dispersal of *Ipomoea pes-caprae* (L.) R.Br. (Miryeganeh *et al.,* 2014; Mircea *et al.,* 2023) and *Ipomoea violacea* L. (Ridley, 1930; Alencar *et al.,* 2021). In *Cuscuta*, the lightweight and small seeds are primarily dispersed by wind or water, facilitating colonisation in areas with abundant vegetation. This long distance seed dispersal is often due to endozoochory by waterbirds, rendering routine quarantine measures to be insufficient in regulating the colonisation of this parasitic plant in new habitats (Costea *et al.,* 2016; Ho & Costea, 2018).

Herbivory and pathogen resistance in Convolvulaceae species, though less studied, are shaped by trade-offs that influence their ecological interactions and coevolutionary patterns. Research within this family indicates that resistance to herbivory is closely linked to pathogen resistance possessing genetic variations that confer quantitative resistance to both insect herbivores and natural pathogens like *Colletotrichum dematium* and *Coleosporium ipomoeae*, suggesting overlapping defence strategies (Simms & Rausher, 1993). Additionally, the trade-offs between resistance and tolerance strategies suggest that while resistance mechanisms can mitigate herbivore impacts, they may also limit plant tolerance to other stresses (Simms & Triplett, 1994). In *Rivea ornata* (Roxb.) Choisy, a rare species, florivory mainly affects non-essential floral structures, such as delicate corolla limbs, while sparing reproductive organs. The presence of latex-producing laticifers in *Rivea* suggests a specialised mechanism that deters florivores from consuming vital floral parts, thereby balancing pollinator attraction with defence. This adaptive strategy enables *Rivea ornata* to maintain high reproductive success despite florivory in this self-incompatible species, which relies entirely on pollinators for reproduction (Chitchak *et al.*, 2024). Nectar production in the extrafloral nectaries of some Convolvulaceae species—structures located at the base of the petiole, pedicel, or sepals—plays a significant role in plant defence (Keeler, 1977; Paz *et al.*, 2016a, b; Chitchak *et al.*, 2022). These nectaries secrete nectar continuously throughout the day and year, attracting a variety of insects, particularly ants (Beckmann & Stucky, 1981; Aguirre *et al.*, 2013). The ants exhibit territorial and aggressive behaviours around these glands, thereby inhibiting or mitigating herbivory and florivory that could compromise floral attractiveness (Keeler, 1980; Silva dos Santos Martins, 2018; Martins, 2020).

A key area of research within the Convolvulaceae focuses on plant-fungal interactions, particularly the symbiotic relationships between certain *Ipomoea* species and clavicipitaceous fungi, such as *Periglandula* (Cook *et al.*, 2019; Beaulieu *et al.*, 2021). Around 450 species within the family are estimated to engage in symbioses with *Periglandula*, which produces ergot alkaloids that are vertically transmitted through seeds. These alkaloids provide critical protection against herbivores and pathogens, highlighting their role in the plant's defence mechanisms. Other alkaloids, such as swainsonine produced by fungi in the order *Chaetothyriales*, and terpenoid indole alkaloids synthesised by the plants themselves, have also been identified as essential defence compounds (Cook *et al.*, 2019). However, research into the diversity of alkaloid-producing fungi and their interactions with *Periglandula* within the Convolvulaceae is still ongoing. Further studies are needed to fully understand the diversity, distribution, and ecological function of these compounds in this plant family.

The ecology of parasitism in the Convolvulaceae reveals a fascinating evolutionary history in *Cuscuta*, the only parasitic genus in this family. A key evolutionary adaptation in parasitic plants like *Cuscuta* is the development of the haustorium, a specialised organ that connects the parasite to its host's vascular system, enabling the transfer of water, nutrients, and even genetic material between the two plants (Yoshida *et al.*, 2016; Fig. 2g). Phylogenetic studies suggest that *Cuscuta* diverged from non- parasitic relatives, with accelerated genome evolution, particularly in terms of gene loss related to photosynthesis, a trait rendered unnecessary by its parasitic nature. Genome reduction has been a hallmark of *Cuscuta* evolution, particularly in terms of plastid gene loss across clades where gene loss reflects the loss of photosynthesis and total reliance on host plants (Braukmann *et al.*, 2013; Sun *et al.*, 2018). The parasitic lifestyle of *Cuscuta* allows it to exploit diverse ecological niches by parasitising a wide range of host plants, including other parasitic plants, affecting the dynamics of plant communities and ecosystems (Stefanović & Olmstead, 2005; Piwowarczyk *et al.*, 2017; Costea *et al.*, 2021).

The ability of Convolvulaceae to adapt to disturbed environments, such as regions with low nutrient availability and high sunlight exposure, is remarkable. This resistance to adverse conditions, combined with rapid life cycles, facilitates the proliferation of various species in agricultural fields. In these environments, species of *Ipomoea* and

Distimake are often considered weeds that compete with soybean, corn, cotton, and sugarcane crops for resources (e.g. Azania *et al.*, 2009; Labonia *et al.*, 2009; Lucio *et al.*, 2011; Chauhan *et al.*, 2012; van Etten *et al.*, 2016; Paul *et al.*, 2023). Some species too are adapted to saline soils, such as *I. pes-caprae*, which thrives in coastal dunes and mangrove areas, where salinity tolerance is crucial for survival (Miryeganeh *et al.*, 2014; Mircea *et al.*, 2023). Moreover, although these flowers are visited by a diversity of animals, they constitute an important resource for the maintenance of local pollinators, especially in human disturbed and urban environments.

3.4 The genomic leap: new data and rapid advances

Convolvulaceae has seen a significant increase in genomic resources in recent years. In terms of nuclear genomes, there are 3 distinct *Ipomoea species* (*I. batatas*, *I. trifida* (Kunth) G. Don, and *I. triloba* L.) and one *Cuscuta* species (*C. australis* R. Br.) with sequenced and annotated genomes. Additionally, a draft genome for the Japanese morning glory (*I. nil*) has been released. As for organellar genomes, numerous chloroplast genomes (43) have been sequenced across the family, providing insights into plastome evolution, structural variations, and gene loss associated with the parasitic lifestyle in *Cuscuta*. Mitochondrial genomes have also been characterised for 17 species, revealing complex structures and potential implications for cytoplasmic male sterility. These genomic resources are key for understanding the evolution and biology of Convolvulaceae, and they will facilitate future research and breeding efforts aimed at improving sweet potato and other species in this family (Supplementary Materials S2, S3).

The most recent phylogenetic study of Convolvulaceae relied on Angiosperms353, with very positive results, and resolving intricate relationships not successfully resolved before, such as the non-monophyly of tribe Merremieae, and the close relationships of *Distimake* with the clade that includes tribe Ipomoeeae (Simões *et al.*, 2022). However, many systematic studies of Convolvulaceae still rely on Sanger sequencing (single gene) studies, as they are less costly than the most advanced genomic techniques. In Convolvulaceae, the largest family phylogenetic study which led to the most recent tribal level classification of the family (Stefanović *et al.*, 2002, 2003), used only chloroplast markers: *rbcL*, *trnL-F*, *atpB,* and *matK*. The initial purpose of the study was to establish the position of *Cuscuta* within the family and, although not successful at this point, it provided an important framework for further systematic studies of the family. A reclassification of tribe Merremieae used both nuclear (*ITS*) and chloroplast markers (*trnL-F*, *matK* and *rps16*), and other molecular systematic studies have tried to follow the same choice of markers, to allow consistency and complementarity of the datasets, as has been done with success in recent studies in *Argyreia* (Rattanakrakang *et al.*, 2022).

Thus, genetic studies in Convolvulaceae come with a degree of challenge, e.g. for DNA extraction, due to the high quantity of phenols. While not all projects seem to find the same level of difficulty, it is not uncommon for researchers to find it challenging to successfully sequence some genetic regions, particularly the longer genes, and most commonly this derives from issues with the DNA extraction, where there is sufficient DNA yield to continue to the sequencing steps, but it is not clean enough, or has high concentration of particular metabolites which interfere with the success of the PCR. The cleaning step of the DNA extraction is of the utmost importance in Convolvulaceae and should be optimised to deal with the presence of phenols, or sugars. Also, there is an abundance of non-coloured or milky sap in some species causing the sticky supernatants during the extraction. A protocol for DNA extraction and single gene markers (primers and PCR conditions) is here proposed (Supplementary Materials S4, S5), to help with the implementation of these techniques in studies involving Convolvulaceae, which could be optimized depending on available reagents or tailored to the taxonomic group being targeted if necessary

3.5 Palynology

As discussed earlier, molecular systematic studies of Convolvulaceae have repeatedly confirmed the value of micromorphological characters for predicting relationships, identify inconspicuous synapomorphies for natural groups, and circumscribe - or correctly place – species, genera, tribes and subfamilies.

Pollen, as an example, has been of extreme importanceinsystematicstudiesofConvolvulaceae, starting with the earliest classification of Hallier, which predicted the division of the family into two major groups: 1) Echinoconieae, having spiny surfaced pollen grains and 2) Psiloconieae, having psilate (non-spiny) pollen grains (Hallier, 1893). Molecular phylogenetic studies have demonstrated that the echinate (spiny) pollen evolved a single time in the family, for which the informal group "Echinoconieae" is monophyletic. However, the remainder of the family possesses almost completely smooth pollen, or bearing micro-spines, and constitutes a paraphyletic group. Echinoconieae currently correspond to tribe Ipomoeeae, and the spiny pollen is a synapomorphic trait for this tribe.

Palynological studies in the tribe Ipomoeeae have consistently reported the unique appearance of spiny pollen, distinguishing this tribe from the others in the family (Hallier, 1893; Sengupta, 1966; Hsiao & Kuoh, 1995; Traiperm, 2002; Tellería & Daners, 2003; Rajurkar *et al.*, 2011; Saensouk & Saensouk, 2018). The pantoporate-type aperture with spines or spinulate processes is applied as a key character of structure and sculpture on pollen in Ipomoeeae. There are two main subtypes of pollen microstructures based on the exine stratification, namely the presence and absence of extraporal regions (Hsiao & Kuoh, 1995). The pollen including tetragonal to hexagonal areas with extraporal regions is likely to be found in the genera *Ipomoea*, *Lepistemon* and *Lepistemonopsis* (Sengupta, 1966; Hsiao & Kuoh, 1995; Tellería & Daners, 2003; Rajurkar *et al.*, 2011; Saensouk & Saensouk, 2018). The pollen features without the extraporal region are found in *Argyreia* and most *Ipomoea* from the Old World (Hsiao & Kuoh, 1995; Traiperm, 2002; Tellería & Daners, 2003; Saensouk & Saensouk, 2018), which could suggest a palynological synapomorphy for subtribe Argyreineae. Various qualitative and quantitative characters on the two subtypes of pollen were also observed that could help palynologically characterise the genera or subtribes within tribe Ipomoeeae, with possible systematic value as synapomorphies for the clades or genera. Pollen of the remaining genera in Ipomoeeae is awaiting to be better studied in order to fully understand the evolutionary relationships among genera and taxa in this tribe, and contribute to a successful generic re-circumscription of this group.

Erdtman (1952) suggested that Convolvulaceae are an eurypalynous family, and that its taxa could be grouped into 'Ipomoea type' and other types. Based on the pollen morphology, the evolutionary trends were also predicted by various studies (Wodehouse, 1935; Sengupta, 1972). Scanning Electron Microscope (SEM) studies were conducted by Kattee *et al.* (2016), who examined 34 species of Convolvulaceae belonging to five genera and studied exine pattern in the Indian Convolvulaceae. Saensouk and Saensouk (2018) studied morphology of pollen grains of 45 taxa belonging to seven genera from Thailand and pointed out that pollens from the Thai Convolvulaceae can be divided into six pollen types based on their aperture viz., Polypantoporate, Hexacolpate, Tricolpate, Periporate, Pantoporate and Zonocolpate (Fig.1).

Studies in the non-spiny members of the family have, thus, revealed important micro-morphological with taxonomic value, such as the number and distribution of apertures, and shape and size of the micro-spines on the surface, supporting genera or morphological groups within the genera, for example *Bonamia* (Moreira *et al.*, 2019), *Cuscuta* (Welsh *et al.*, 2010), *Decalobanthus*

(Simões *et al.,* 2021), *Jacquemontia* (Buril *et al.*, 2014), *Operculina* (Simões *et al.,* 2019) and*Xenostegia* (De Man & Simões, 2021). In general, pollen characters have shown to be of high predictive value, for example to determine species assignment to a given genus/subgenus which has proven to be supported by molecular phylogenetics (Ferguson *et al.,* 1977; Sosef *et al.,* 2019). Exceptionally, cases of evolutionary convergence have been reported, for example in *Distimake Vitifolius* (Burm.f.) Pisuttimarn & Petrongari, a species which presented 6-zono- colpate pollen type that was considered diagnostic of genus *Camonea*, and therefore the species was transferred to this genus (as *Camonea vitifolia* (Burm.f.) A.R.Simões & Staples) which later, more robust, molecular phylogenetic studies proved not be the case, but belonging in *Distimake* instead, where such pollen type was not yet documented (Pisuttimarn *et al.,* 2023). Such cases are rare in Convolvulaceae, where pollen most commonly has high systematic predictive value, but it needs to be considered that such value of palynological characters should be continuously evaluated in an evolutionary framework.

3.6 Anatomy

Anatomically, Convolvulaceae are also one of the families that are best characterised. As overall features, the presence of two vascular variants, the intraxylary phloem (Fig. 2a-c) and the successive cambia (Fig. 3a) make it unique in the angiosperms. Another conspicuous feature is the presence of laticifers (Fig. 2b, d), which are articulated, non-anastomosing (Fahn 1979; Carlquist & Hanson 1991; Ceja-Romero & Pérez-Olveda, 2010), producing a white or yellowish exudate. These laticifers are present in the cortex, pith (Fig. 2b), secondary phloem (Fig. 2d), and conjunctive tissue. In the secondary xylem, vessels may be solitary or in multiples (Fig. 2a, c-e, H), being either radial or tangential multiples (Fig. 2a, c-e, h). Tyloses are very common in the vessels, and they may be either regular (Fig. 2d, h) or sclerotic (Fig. 2e). Another extremely common feature is the presence of the entire gradation of imperforate tracheary elements, i.e., true fibres, fibre-tracheids, and true tracheids (*sensu* Carlquist, 2001; Olson, 2023; Fig. 2f), commonly co-occurring (Carlquist & Hanson, 1991). Axial parenchyma is typically paratracheal, vasicentric to aliform (Fig. 3c, e), with or without short confluences, commonly also in patches, the latter non-lignified (Fig. 2h). Rays of two different sizes are typically present in the lianas, the uniseriate, short rays and the wide, multiseriate rays (Fig. 2i). The uniseriate rays are lignified (Fig. 2f, i), while the wide rays are non-lignified (Fig. 2i). The latter connects to the conjunctive tissue, interconnecting the different successive cambia (Fig. 2a). Non-lignified parenchyma is very common in the species with successive cambia (Fig. 2a, h). Sometimes the entire stem and root fissures due to parenchyma proliferation (Carlquist & Hanson, 1991). Druse crystals are present both in axial (Fig. 2h) and ray parenchyma, sometimes also within the tyloses (Carlquist & Hanson, 1991). Amiloplasts are extremely common in all parenchymatic tissues (Cejas-Romero & Pérez-Olveda, 2010), both in tissues of primary and secondary origin (Fig. 2b). The secondary phloem has sieve tubes solitary or in radial rows (Fig. 2d), sieve plates simple to compound, and in most species the phloem is devoid of sclerenchyma (Fig. 2d), although clusters of sclereids sometimes are formed in the nonconducting phloem. Below we give additional information on the vascular variants that are so conspicuous to the family.

Intraxylary phloem (Fig. 2b-c) is probably the most commented shared anatomical feature of the Convolvulaceae, and it has been used to support their relationship to the Solanaceae (Schenck, 1893; Solereder, 1908; Metcalfe & Chalk, 1950; Stevens, 2001 onwards). If indeed intraxylary phloem is a synapomorphy of the clade [Convolvulaceae, Solanaceae], its absence in *Humbertia*, *Cuscuta* (Fig. 2g) and a few members of *Convolvulus* (e.g., *Convolvulus floridus* L.f. from the Canary Islands, pers. obs.) represents independent loses. The intraxylary phloem in Convolvulaceae is derived from bicollateral vascular bundles (Metcalfe & Chalk, 1950). However, it is very common that during development, an internal vascular cambium is formed between the protoxylem and the primary intraxylary phloem, giving rise to secondary phloem towards the centre of the pith (Fig. 2c) and secondary xylem towards the protoxylem, obliterating the entire pith (Carlquist & Hanson, 1991; Rajput *et al.*, 2008, 2013; Patil *et al.*, 2009; Rajput & Gondaliya, 2017). Sometimes these secondary growth increments are termed inversed vascular bundles, but this is a misnomer, since the term vascular bundle should be used exclusively to primary structure. Successive cambia have been recorded in more than 10 genera of the family (*Argyreia, Calonyction* Choisy, *Convolvulus, Dicranostyles, Distimake, Erycibe, Hewittia, Ipomoea, Maripa, Merremia, Porana* Burm.f. and *Rivea*; Metcalfe & Chalk, 1950, Carlquist, 2001); however, some of these previously cited genera have been merged into *Ipomoea* (e.g., *Calonyction* and *Rivea*). Successive cambia are originated in the outer limits of the vascular cylinder, in the pericycle (Terrazas *et al.,* 2011), which corresponds to the master cambium of Carlquist (Carlquist, 2007). The pericycle divides in many rows forming a parenchymatic band of variable thicknesses. Within this band, a new cambium is formed. This new cambium starts producing secondary xylem and phloem, enclosing parts of this previously proliferated parenchyma, which will now be recognised as conjunctive tissue. The conjunctive tissue, being parenchymatous and nonlignified, connect successive cambia and may give rise to yet new cambia at later stages. These new cambia can develop with either regular or opposite orientations, in the latter producing xylem to the outside of the stem and phloem to the inside (Rajput *et al.*, 2008, 2013). A broad scale anatomical studies of the entire Convolvulaceae is needed to understand when the successive cambia appeared in the family and how they diversified. In the genera where they are present, they are present in lianas, shrubs, and trees (e.g., *Ipomoea* series *Arborescentes*; McDonald, 1992; Ceja-Romero & Pérez-Olvera, 2010; Terrazas *et al.,* 2011). In trees of the *Ipomoea* series *Arborescentes*, the number of successive cambia goes much beyond that of lianas (Carlquist & Hanson, 1991), while in the commonly cultivated shrub *Ipomoea carnea*, new cambia appear only in very advanced phases of secondary growth, sometimes even being recorded as absent (McDonald, 1992). Successive cambia are thought to increase the flexibility in climbers, while in the *Ipomoea* series *Arborescentes* they may act as a storage tissue (*pers. obs.*) similarly to what suggested for the roots (Artschwager, 1924). The successive cambia of roots cause complete breakdown of the secondary tissues (Fig. 3a), by forming concentric cambial islands which produce a few xylem vessels inwards and phloem parenchyma outwards (Fig. 3b), with an enormous amount of amiloplasts (Fig. 3b; Artschwager, 1924). Regarding the leaves, the main veins have typically bicollateral vascular bundles (Fig. 3c-e), with or without a fibrous cap (Fig. 3c-d). The paradermal section of the leaf epidermis shows cells walls can be straight or curved (Solereder, 1908) or sinuated in *Argyreia* (Traiperm *et al.,* 2017). The blades display a single epidermal layer to both sides. (Fig. 3c-d). Tanniniferous epidermal cells are common in the adaxial epidermis (Solereder, 1908; Ketjarun *et al.,* 2016; Fig. 3f-g). The mesophyll is heterogeneous, dorsiventral (the most common; Fig. 3f) or isobilateral (dominant in genera like *Convolvulus, Evolvulus, Cressa*; Metcalfe & Chalk, 1950; Fig. 3g). In the dorsiventral mesophyll it is common to find a palisade parenchyma and spongy parenchyma (Fig. 3f), but sometimes the spongy parenchyma is poorly developed to isobilateral (e.g., *I. pes-caprae*; Fig. 3g), and palisade and spongy cells are different in shape. The vascular bundles on the mesophyll are either collateral (Fig. 3f-g) or bicollateral. Laticifers can be present in the cortex of the main veins and throughout the mesophyll, commonly associated to the vasculature (Fig. 3f-g). The presence of crystalliferous idioblasts with druses of different forms and sizes is widespread (Solereder, 1908; Fig. 3g).

3.6. Root development and genetics

What is the function of storage roots in Convolvulaceae? What nutrients do they store? How do they do form? How have they evolved? How to they develop? Evolution and formation of storage roots in sweet potato and its wild relatives (mainly within genus *Ipomoea*) are a source of numerous research questions that we are only now just starting to unfold, with the integration

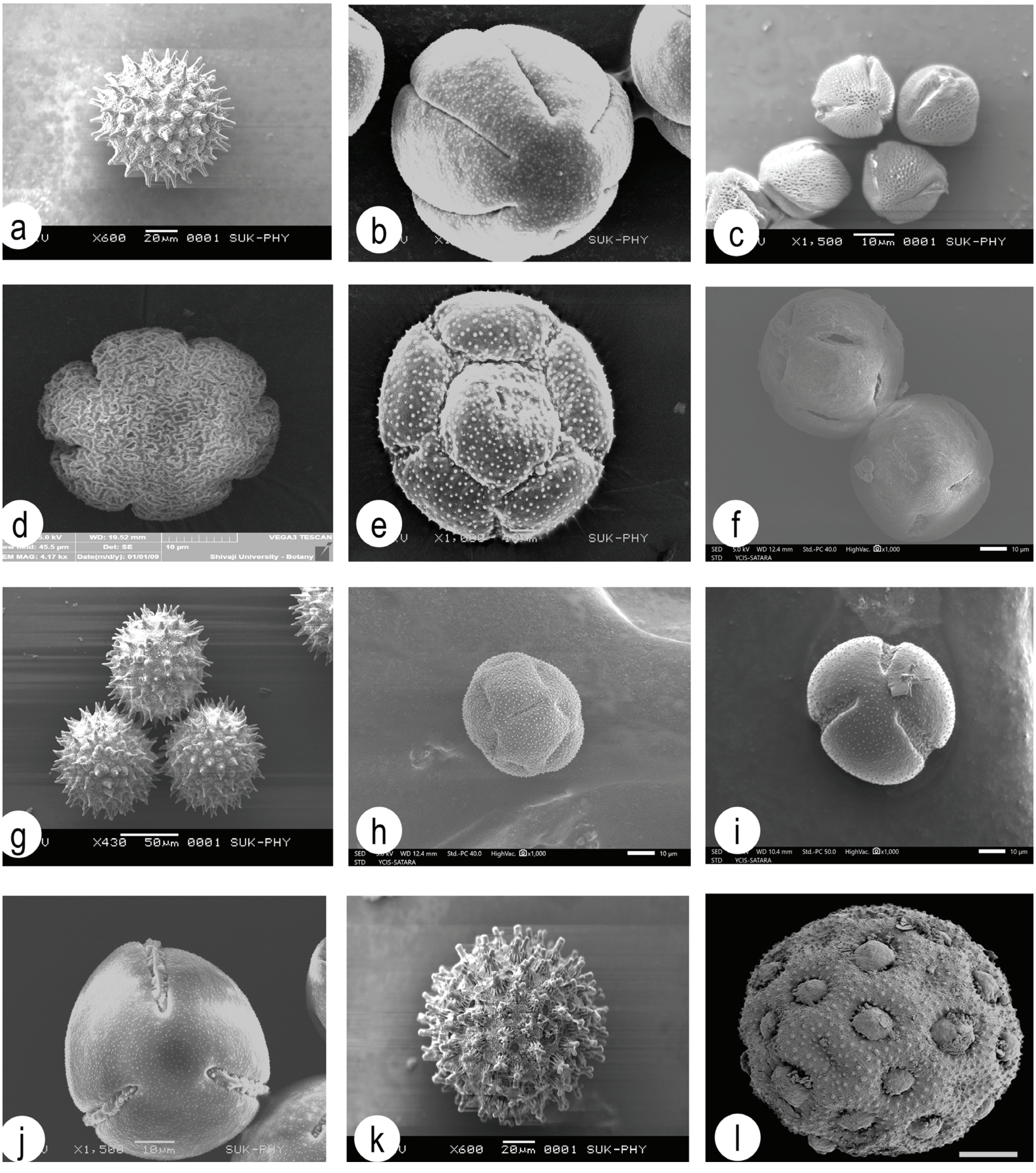

Fig. 1. Pollen diversity of Convolvulaceae: **a**. *Argyreia nervosa* (Burm.f.) Bojer, **b**. *Camonea umbellata* (L.) A.R. Simões & Staples, **c**. *Convolvulus arvensis* L., **d**. *Cuscuta reflexa* Roxb., **e**. *Distimake tuberosus* (L.) A.R. Simões & Staples, **f**. *Hewittia malabarica* (L.) Suresh, **g**. *Ipomoea clarkei* Hook.f., **h**. *Jacquemontia pentanthos* (Jacq.) G. Don, **i**. *Merremia hederacea* (Burm.f.) Hallier f., **j**. *Operculina turpethum* (L.) Silva Manso, **k**. *Rivea ornata* (Roxb.) Choisy, **l**. *Xenostegia trdentata* (L.) D.f. Austin & Staples.

of genomic, transcriptomic, anatomic and developmental studies, and are much necessary to be expanded at family level, considering many other species outside of genus *Ipomoea* (i.e. *Decalobanthus, Distimake, Operculina*) also develop storage roots.

Evolutionary studies in selected species of morning glories (*Ipomoea*) have demonstrated that storage roots have evolved at least ten times, independently, within Convolvulaceae, and that different species of morning glories are anatomically different but utilize a common core set of genes in storage root formation, consistent with a pattern of parallel evolution. This also highlights the importance of combining anatomy together with gene expression to understand the evolutionary origins of ecologically and economically important plant traits (Eserman *et al.*, 2018; Vanderschuren & Agusti, 2022).

The root system architecture (RSA) of plants, which includes structural features like root length, spread, number, and length of lateral roots, exhibits great plasticity in response to environmental changes (Khan *et al.*, 2016). This plasticity could be critical to developing crops with more efficient roots that can better tolerate abiotic stresses like drought (Khan *et al.*, 2016). Much of the research on root traits has focused on major cereal crops, but understanding root architecture in Root and Tuber Crops (RTC) like sweet potato (*I. batatas*) is of paramount importance (Villordon *et al.*, 2014; Duque & Villordon, 2019). Sweet potato is a major RTC, and its RSA is known to be highly variable and responsive to environmental factors like nutrient availability (Duque & Villordon, 2019; Villordon *et al.*, 2020; Villordon & Gregorie, 2021). Studies have shown that specific root branching traits in sweet potato can confer enhanced nutrient acquisition, and these traits are being incorporated into breeding populations (Villordon & Firon, 2016; Duque & Villordon, 2019; Villordon *et al.*, 2020). However, the understanding of root branching and its relationship to productivity in sweet potato has lagged behind other crops (Duque & Villordon, 2019).

Early root development and branching are particularly important in sweet potato, as they influence the onset and development of storage roots, which are the economically important product (Villordon *et al.*, 2012; Duque, 2024; Villordon, 2024). Researchers have used various techniques like root scanning, image analysis, and X-ray computed tomography to study sweet potato root architecture, especially at the onset of storage root formation (Villordon & Clark, 2018; Singhvi *et al.*, 2022). These studies have revealed that factors like nutrient availability, pathogen infection, and heavy metal stress can significantly alter sweet potato root architecture, including root length, lateral root development, and root branching (Villordon *et al.*, 2013; Villordon & Clark, 2018; Villordon *et al.*, 2020; Villordon & Gregorie, 2021; Villordon, 2024). For example, one study found that variation in phosphorus (P) availability altered root length and lateral root development in two sweet potato cultivars at the onset of storage root formation (Villordon *et al.*, 2020). Another study showed that the presence of arsenic (As) exerted a profound effect on root architecture that was tightly coordinated with the plant's detoxification machinery (Villordon, 2024). Additionally, boron (B) availability was found to alter root architectural attributes like root length, surface area, and volume at the onset of storage root formation in three sweet potato cultivars (Villordon & Gregorie, 2021).

Researchers have also explored the genetic and molecular mechanisms underlying root architecture in sweet potato. Studies have identified nutrient-responsive genes related to root system architecture variability and storage root formation (Villordon & Firon, 2016), as well as the role of auxin in regulating root architecture in response to potassium deficiency (Liu *et al.*, 2023).

The RSA of sweet potato is a critical trait that exhibits significant plasticity in response to environmental factors. Understanding the genetic and molecular mechanisms underlying

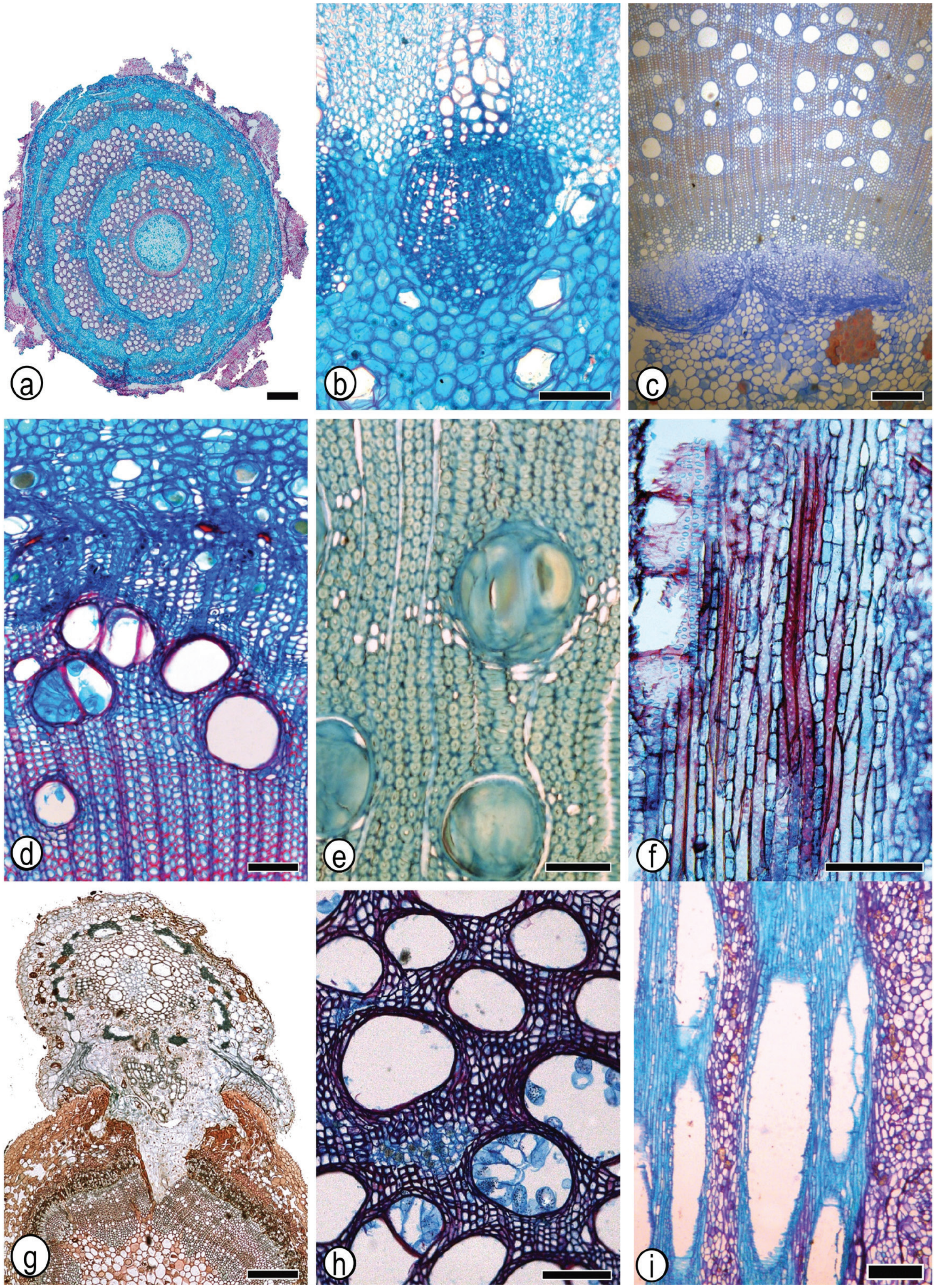

Fig. 2. Key anatomical characteristics of Convolvulaceae. Images showcase the distinctive presence of intraxylary phloem (**a**-**c**) and successive cambia (**a**), features that set the family apart within angiosperms. Articulated, non-anastomosing laticifers, which produce a white or yellowish exudate, are evident tissues cortex, pith and secondary phloem (**b**,**d**). Vessel solitaryor in radial and tangential multiples (**a**, **c**-**e**, **h**), and the presence of tyloses—both regular (**d**, **h**) and sclerotic—are shown. Also depicted are gradations of imperforate tracheary elements (**f**), paratracheal axial parenchyma (**c**, **e**), uniseriate (**f**) and multiseriate rays, sometimes co-occurring (**i**), and non-lignified conjunctive parenchyma in species with successive cambia (**a**, **h**). Additional features include druse crystals in parenchyma (**h**) The parasitic species are unique in lacking intraxylary phloem and successive cambia. (**g**). Species: (**a**, **f**) *Ipomoea sericosepala*, (**b**) *I. murucoides*, (**c**) *Maripa glabra*, (**d**) *I. arborescens*, (**e**) *Humbertia madagascariensis*, (**g**) *Cuscuta* sp., (**h**) *I. saopaulista*, (**i**) *I. cairica*. Scale bars: A = 2mm, B, F-G, I = 200 µm, C = 300 µm, D-E = 100 µm, H = 150 µm.

root architecture, as well as developing non-destructive phenotyping techniques, will be crucial for breeding and managing these crops to improve productivity and abiotic stress tolerance, namely in sweet potato but also with a focus on its wild relatives that also present storage roots (Villordon *et al.*, 2014; Khan *et al.*, 2016; Duque & Villordon, 2019; Singhvi *et al.*, 2022).

4. Keeping up with Convolvulaceae: reference collections, databases and specialists' network

Herbaria are key repositories of biodiversity (Besnard *et al.,* 2018) and herbarium specimens are essential for preserving morphological characteristics of the plants, holding important ecological, ethnobotanical and geographic information, and as a source of material for phenological, phytochemical, micromorphological or molecular studies (Funk, 2003; Nesbitt, 2014; Heberling *et al.,* 2019). Hence, herbarium collections are of vital importance for studies of Convolvulaceae, from providing morphological, geographic, ecological and historical information to being an essential source of samples for anatomical, palynological, chemical and molecular studies.

The largest number of herbarium collections for Convolvulaceae are housed at MO – Missouri Botanical Garden (43,470), RB – Jardim Botânico do Rio de Janeiro (Brasil) (42,282) and MEXU –Universidad Nacional Autónoma de México (39,365). While MO offers a global representativity of the family, RB (Jardim Botânico do Rio de Janeiro) and MEXU's (Universidad Nacional Autónoma de México) collections of Convolvulaceae are mainly focused on Brazil and Mexico, respectively. Other important global collections are P – Paris Herbarium (37, 485), US – Smithsonian Institution (23,715 records), Naturalis (L, U and WAG) (28,321), BR – Meise (17,550) and K – Kew Herbarium (14,198) (https://gbif.org, Accessed December 2024).

In addition to preserved specimens, a large living collection can also be found in Paris (France), the Collection Nationale des Convolvulacées (https://www.ccvs-france.org/les-collections/lannuaire-des-collections-du-ccvs/convolvulaceae). Founded in 1996 by Patrick Blanc as a collection of ornamental plants, and currently managed by Me. Nelly Bouilhac, this collection has grown as an important centre of ex-situ conservation and seed bank for rare and endemic species of Convolvulaceae. It currently houses over 360 species, belonging to 31 genera. The park where it is inserted is open to the general public, and the living collections have more restricted access but can also occasionally be visited. Access to visiting scientists is permitted, as well as destructive sampling, by arrangement with the direction of the collection. Seeds can also be exchanged or requested.

Taxonomic databases such as Plants of the World Online (https://powo.science.kew.org), Tropicos (https://tropicos.org), and the World Flora Online (https://worldfloraonline.org) are reliable sources of information for the current taxonomy of the family, with regular maintenance and good interface with other sources of data (geographic, nomenclature, and digital specimens). For more specialised information on the family, the website Convolvulaceae Unlimited (https:// convolvulaceae.myspecies.info) is an important reference, rich with literature, images and exclusive information on the species' taxonomy, distribution or conservation status; this has, unfortunately, been discontinued, and is no longer being regularly updated, but it provides extraordinary volume and quality of data, having been verified by specialists in the family. Currently, an active network of researchers working on several research questions and applications involving Convolvulaceae exists ("Convolvulaceae Network"), which can be contacted for queries, exchanges or opportunities for collaboration (address: convolvulaceae.network[at]gmail.com).

5. Best Practices and recommendations

5.1. Field Collection

When collecting Convolvulaceae in the field, it is important to adequately preserve morphological and reproductive characters, to enable the best

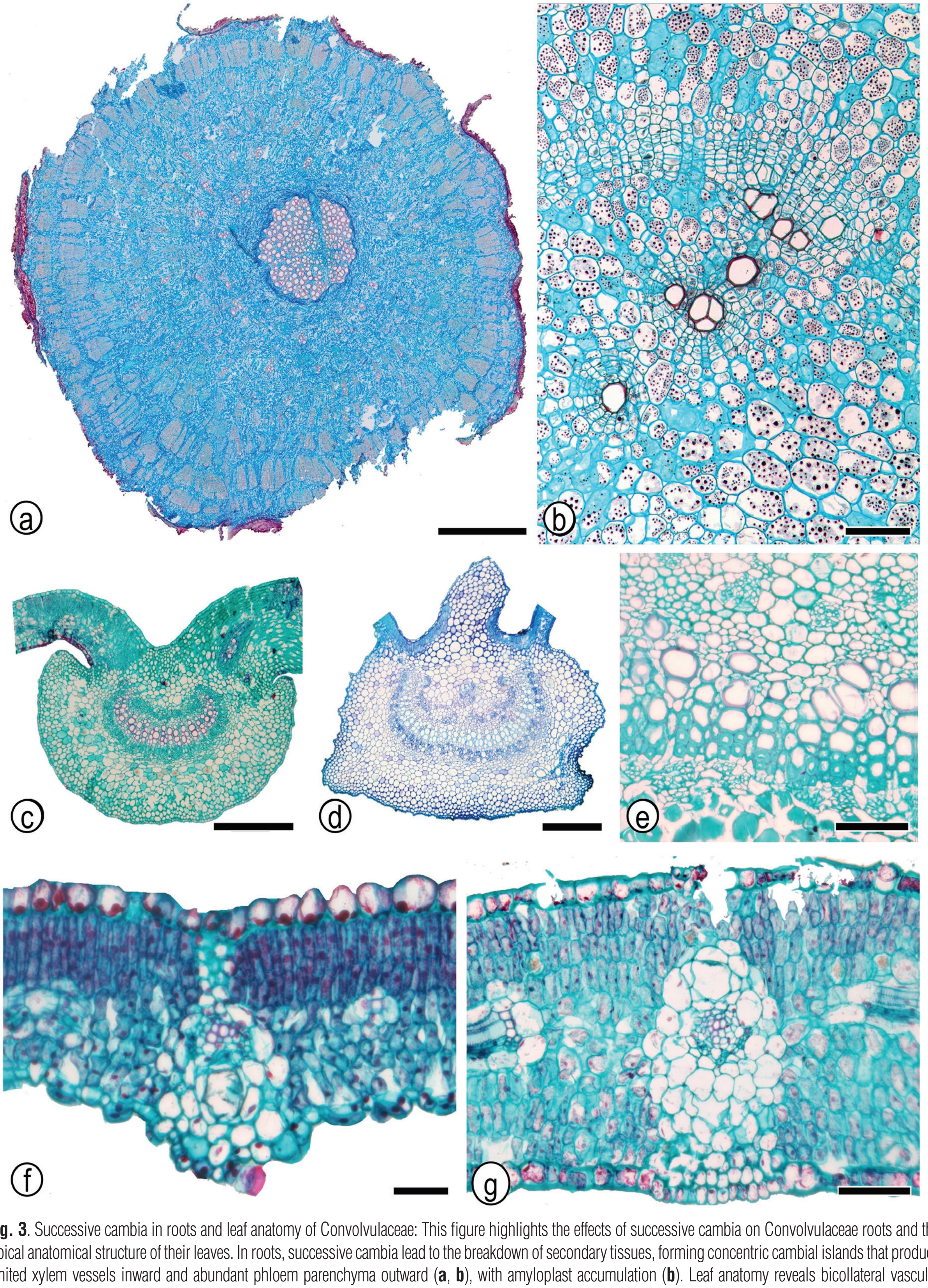

Fig. 3. Successive cambia in roots and leaf anatomy of Convolvulaceae: This figure highlights the effects of successive cambia on Convolvulaceae roots and the typical anatomical structure of their leaves. In roots, successive cambia lead to the breakdown of secondary tissues, forming concentric cambial islands that produce limited xylem vessels inward and abundant phloem parenchyma outward (**a**, **b**), with amyloplast accumulation (**b**). Leaf anatomy reveals bicollateral vascular bundles in main veins, with or without fibrous caps (**c**-**e**). The epidermal cell walls vary in shape (c-d), and tanniniferous cells are common in the adaxial epidermis (**f**-**g**). Leaves typically have dorsiventral or isobilateral mesophyll (**f**-**g**), with palisade and spongy parenchyma differentiated in the former (**f**). Laticifers, often near vascular bundles, and crystalliferous idioblasts with druses are also present (**f**-**g**). Species: (**a**) *Ipomoea bonsai*, (**b**) *I. batatas*, (**c**) *I. murucoides*, (**d**) *I. saopaulista*, (**e**) *I. coriacea*, (**f**) *I. sericosepala*, (**g**) *I. pes-caprae*. Scale bars: A = 5 mm, B = 300 µm, C-D = 400 µm, E = 200 µm, F = 50 µm, G = 100 µm.

of their use in subsequent studies. Based on accumulated experience from working with this plant family, we recommend to adopt the following practices, when collecting in the field:

- **Collect all elements of the plant**, including underground organs (root, stem, inflorescences, fruits and seeds): roots are ofte forgotten to be collected, and for this reason there is incomplete knowledge of root systems across the family (Fig. 4).
- **Document the habit:** After the plant has been pressed and dried, it is more difficult to evaluate if the live plant was climbing, prostrate or erect (shrub or sub-shrub); photographing and annotating habit characteristics onto the specimen label is very helpful for correct species identification and future studies.
- **Press flowers carefully for future preservation**: Carefully cushion the flowers in between greaseproof paper, wax paper, coffee filters, or an absorbent material (e.g. tissue or toilet paper); flowers of Convolvulaceae are very fragile and easy to wilt and glue to other materials, when pressed; involving them in greaseproof paper, or an absorbent material, will avoid the flower getting in touch with the newspaper in which field plants are normally collected, and will better preserve features like shape or colour.
- **Dissect flower in the field**: Most of the times, flowers are dissected when examined in the herbarium; however, as flowers of Convolvulaceae are so fragile, re-hydration and dissection from herbarium specimens are very challenging; a good tip is to already press a dissected flower in the field; for this, open a flower in the field, and press it open in greaseproof paper or absorbent material, in a way that internal characters of the flowers are easily visualised, such as anthers, filaments, style, stigma and ovary.
- **Collect flowers in alcohol**: As flowers of Convolvulaceae are very fragile and deliquesce quickly, especially in the heat, they do not preserve their shape or texture, hence it is important to photograph and collect the flower in alcohol; fruits and other parts of the plant tend to preserve well when pressed and dried, and are not necessary to preserve in alcohol.
- **Liquid preservation of soft tissues:** If intending to perform anatomical studies, always liquid preserve the collected organs (either roots, stem, or leaves). Liquid preservation is needed since Convolvulaceae typically contain lots of soft, parenchymatic

Fig. 4. Pressing Convolvulaceae plants for herbarium specimens: To enhance the utility of Convolvulaceae specimens in research, certain collection and preservation methods are recommended. Collect all parts of the plant, including underground organs, to provide a complete representation of the species. Document the plant's growth habit (climbing, prostrate, or erect) with field notes and photographs. For delicate flowers, press between absorbent materials, ideally opening one flower to reveal internal structures like the ovary and style, essential for taxonomic identification. Collect flowers in alcohol to preserve their shape and texture, while fruits and other parts can be pressed directly. For anatomical studies, liquid preservation is advised to prevent tissue collapse, using standard fixatives or 70% ethanol as a substitute. Collecting specimens both in flower and fruit aids identification, as sterile Convolvulaceae are difficult to classify to genus or species level. Following these guidelines ensures specimens retain key characteristics, maximizing their research value.

tissues that collapse when dried. Commonly used fixatives are best (FAA 50, Johansen 1940), but in the absence of these, 70% ethanol will suffice. For anatomical sectioning, we recommend embedding the samples in polyethylene glycol 1500 and using a polystyrene resin coat while sectioning in the sliding microtome (Barbosa *et al.*, 2010).

5.2 Photography and illustration

Photograph or draw important details of floral morphology. Floral characters such as style, stigma, ovary, sepal shape and texture, colour and indumentum of mid-petaline bands, and corolla colour and shape, are critical for species identification in Convolvulaceae; once plants are pressed and dried onto herbarium sheets (and sometimes glued or sown), it is very difficult to recover some of these details accurately, therefore photographing, drawing them or describing them in the field can be very helpful.

Important features to visually document in the field (photograph or draw) are (Fig. 5):

- Frontal view of the corolla showing corolla shape and colour (Fig. 5a).
- Lateral view of the corolla, showing inflorescence structure, shape and size of bracteoles and sepals, shape and size of the corolla (Fig. 5b).
- Internal view of the corolla, showing ovary, style, stigma, filaments (including indumentum and insertion on the corolla) and anthers (Fig. 5c, 5d).
- "Tilted" front view of the corolla: a slightly angled photo of the corolla from above will help capture the inside of the corolla tube, including stamens, style and stigmas (Fig. 5e, 5f).
- Habit (Fig. 5g).

The future of Convolvulaceae studies: the next frontiers

Building on the synergetic momentum that has been generated, we look ahead at the next frontiers

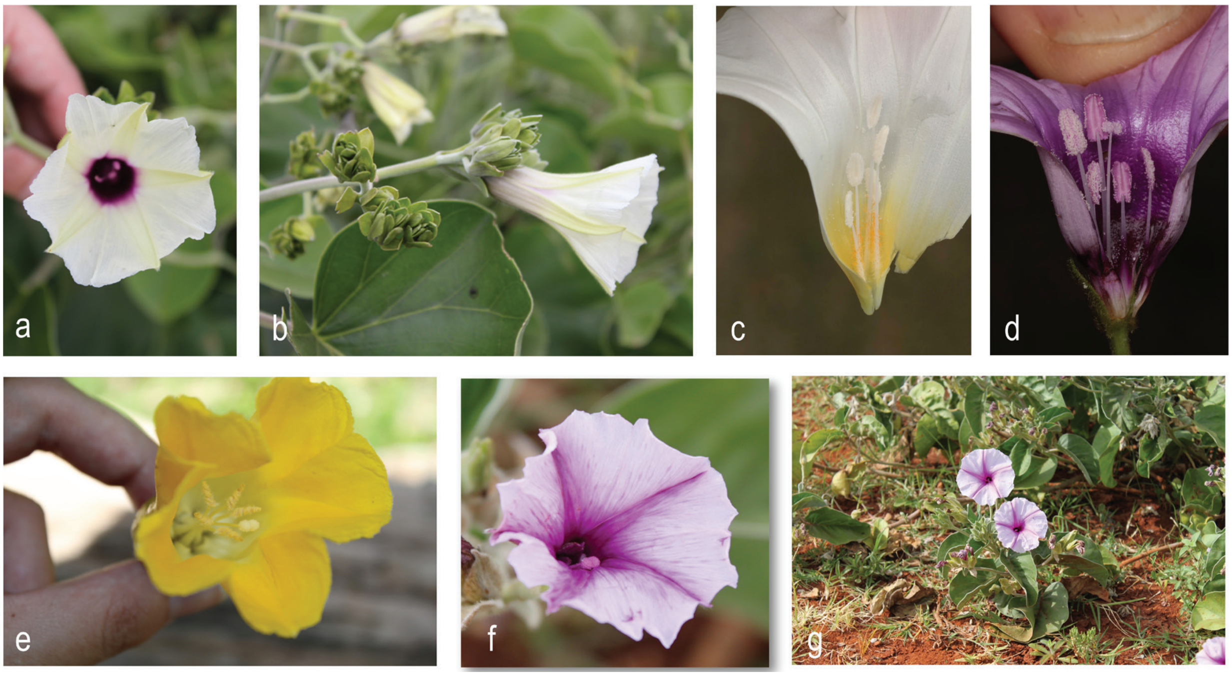

Fig. 5. Photography elements that help with Convolvulaceae identification: **a**. Frontal view of the corolla showing corolla shape and colour; **b**. Lateral view of the corolla, showing inflorescence structure, shape and size of bracteoles and sepals, shape and size of the corolla; **c** & **d**. Internal view of the corolla, showing ovary, style, stigma, filaments (including indumentum and insertion on the corolla) and anthers; e & f. "Tilted" front view of the corolla: a slightly angled photo of the corolla from above will help capture the inside of the corolla tube, including stamens, style and stigmas; g. Habit. Species: **a** & **b**. *Ipomoea kitueinsis* Vatke; **c**. *Ipomoea tricolor* Cav.; **d**. *Ipomoea wightii* (Wall.) Choisy (photo L. Chatrou); **e**. *Decalobanthus peltatus* (L.) A.R. Simões & Staples; **f**.: *Ipomoea hildebrandtii* Vatke; **g**. *Ipomoea hildebrandtii* Vatke (photo A. Simões).

of knowledge in this economically important – and fun – plant family. Through the integration of different sources of evidence and international and multidisciplinary collaborations, there is an opportunity to finally grasp long standing overarching challenges in this plant family, both related to its useful and non-useful plants. Within the next five to ten years, we expect that the following objectives will be the main priorities for Convolvulaceae research:

- Produce a well-resolved, strongly supported, family-level phylogeny of the family;
- Produce an improved classification of the family, solving the uncertainties of relationships between subfamilies and tribes;
- Re-classify tribe Ipomoeeae;
- Resolve the tribal and generic delimitation within the "bifid style" clade (Dichondroideae/Dicranostyloideae);
- Resolve the position of *Cuscuta* and *Erycibe* in the family;
- Elaborate on biogeographic, diversification and evolutionary processes at family scale;
- Understand the evolution of pollen, fruits and root characters;
- Improve our understanding of storage root formation and evolution, as well as the genetic mechanisms behind them;
- Monograph and taxonomically revise at least 30% of the genera, incorporating multiple sources of data;
- Describe new species and solve species complexes, especially in highly diverse and understudied regions and genera, where there is greater potential for undescribed taxa;
- Compile worldwide information on food, medicinal and cultural applications;
- Assess the conservation status of at least 30% of the species of the family;
- Understand the unique plant-fungi associations in Convolvulaceae and their effect in the production of specialised metabolites.

As a community, we will strive to:

- Generate and regularly maintain shared global datasets, through the Convolvulaceae Network community, Convolvulaceae Unlimited website or other available resources;
- Contribute to the update and accuracy of existing taxonomic reference databases (e.g. POWO and WFO);
- Enhance international partnerships and multidisciplinary projects, including jointly applying for funding proposals at national and international scales;
- Train a new generation of Convolvulaceae specialists that will work collaboratively across borders and with integrated methodologies.

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