Structural Diversity of Flowers and Pollination Ecology in Podostemaceae

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Abstract: Podostemaceae, or "river-weeds," are a diverse family of freshwater angiosperms adapted to fast-flowing tropical and subtropical rivers. With over 300 species, they exhibit remarkable morphological variation across regions, especially between New World and Old-World taxa. Their life-cycle is tightly synchronized with seasonal water levels, with flowering and seed production occurring as waters recede. These plants rely solely on sexual reproduction, making pollination a key evolutionary driver for diversification. Different pollination strategies, melittophily, anemophily, and self-pollination have been reported within the family. However, integration of floral morphology and pollination biology remains limited. Thus, an overview of reproductive characters in Podostemaceae is presented, focussing on characters that are useful in understanding the pollination strategies and functional floral morphology in the family. This review synthesizes current knowledge to explore how pollination systems and floral traits have shaped the evolutionary trajectory of Podostemaceae.

Keywords: Aquatic angiosperms, evolution, floral biology, perianth, spathella, pollination diversity

Introduction

Podostemaceae, widely known as "river-weeds", are a vast family of unique haptophytic fresh water angiosperms. These plants grow in the tropical and sub-tropical regions of the world with a few species in temperate regions (Cook & Rutishauser, 2007; Koi *et al.,* 2015). Podostemads

grow in fast-flowing waters of rivers, rapids or cataracts, clinging tightly to the rocks with the help of small haptera or holdfasts and adhesive hairs. The life cycle of these plants is closely correlated with changes in water level in the rivers. During the rainy season, plants remain in vegetative state and produce underwater flower buds in the early dry season. As the water recedes, flowers open and undergo fertilization to produce seeds in capsule (Mohan Ram & Sehgal, 1992; Koi *et al.,* 2015).

With more than 50 genera and 300 species, Podostemaceae is the largest family of fresh water angiosperms. The family is placed in the eudicot order Malpighiales and is sister to Hypericaceae (Wurdack & Davis, 2009; Ruhfel *et al.,* 2011). Podostemaceae are divided into three subfamilies, *i.e.,* Podostemoideae, Weddellinoideae and Tristichoideae (Koi *et al.,* 2015). Among these, Podostemoideae is the largest, and categorised into various clades distributed across different geographic regions, *i.e.,* taxa from Africa, Asia/Australia and the Americas (except *Podostemum* Michx.) (Koi *et al.,* 2012). All Tristichoideae genera (except *Tristicha* (Bory ex Willd.) Spreng. and *Terniopsis* H.C. Chao) are restricted to Asia (Kato, 2006; Koi *et al.,* 2022) and Weddellinoideae is a monotypic subfamily that occurs in Suriname, Guiana, Venezuela, Colombia, and Brazil (Cook & Rutishauser, 2007).

Within the family, there is a marked diversity with regard to size and the number of various plant

parts. Generally, the New World podostemads are larger and more conspicuous than their Old World counterparts. The differences are reflected not only in the vegetative structures but also in the number of floral organs. In the Asian Podostemoideae, shoots are unbranched and short (≤1 cm long) (Cusset, 1992), whereas many African and American members of this subfamily form elongate and branched shoots, exceeding over 80 cm in length (Cusset, 1987). Similarly, leaves may be simple and thread like as in the Asian Podostemoideae or compound with coiled pinnae as in the American Podostemoideae. The New World podostemads bear numerous, large, polysymmetric and multistamenous flowers arranged in an inflorescence whereas those of the Old-World bear solitary, small, monosymmetric flowers with only two stamens.

The evolution of pollination systems has been pivotal to the ecological and evolutionary success of angiosperms. While most aquatic plants have retained the pollination mechanisms of their terrestrial ancestors—systems not originally adapted to function in aquatic environments—some lineages have acquired novel traits that enable pollination under water, giving rise to hydrophily (Cook, 1988; Sculthorpe, 1967). The repeated and independent origins of hydrophilous pollination underscore the continuing importance of sexual reproduction in the diversification and persistence of aquatic plants (Philbrick & Les, 1996).

Among the aquatic angiosperms, Podostemaceae is unique in lacking any form of asexual reproduction, relying exclusively on sexual reproduction for perpetuation. This renders the pollination event an especially critical ecological and evolutionary determinant of reproductive success in podostemads. A wide spectrum of pollination strategies has been documented in the family, ranging from melittophily, anemophily to self-pollination (Philbrick, 1984; Khosla & Mohan Ram, 1993; Lobreau-Callen *et al.,* 1998; Khosla *et al.,* 2000, 2001; Okada & Kato, 2002; Cook & Rutishauser, 2007; Sehgal *et al.,* 2009; Gupta &

Sehgal, 2009; Sobral-Leite *et al.,* 2011; Khanduri *et al.,* 2014; da Silva Batista *et al.,* 2020, 2021; Khanduri *et al.,* 2024).

Despite these generalities, much of the available evidence is scattered, and morphological and pollination data have rarely been integrated into a unified framework. A comprehensive knowledge of floral morphology in relation to pollination will help to improve understanding of evolutionary trajectories in Podostemaceae. In this review, we examine floral morphology and synthesize available studies on pollination biology in the family, with the aim of elucidating the evolutionary dynamics that have shaped Podostemaceae.

Perianth

The three subfamilies of Podostemaceae are primarily distinguished by the presence and structure of the perianth. In Podostemoideae, the perianth is generally absent, except in some New World taxa where it is represented by a complete whorl of linear, spathulate, or tooth-like tepals surrounding the ovary. For example, in *Mourera* Aubl., 8–15 triangular or lanceolate tepals occur (Sobral-Leite *et al.,* 2011), whereas in *Marathrum* Bonpl. the flowers bear 7–9 minute, triangular, deciduous, green, inconspicuous, scale-like tepals alternating with the stamens (Pérez-Pacheco *et al.,* 2024). The term 'tepal' has also been applied by several authors to the filiform structures situated on either side of the stamens (Sculthorpe, 1967; Rutishauser, 1997; Cook & Rutishauser, 2007). Morphological and developmental evidences, however, demonstrate that these structures are staminodes, not true tepals: they occur in the same whorl as the stamens, develop nearly simultaneously with them, and represent stamens lacking anthers (Khosla & Mohan Ram, 1993; Sehgal *et al.,* 2009; Kato *et al.,* 2022). Thus, they are not homologous with the true tepals of Tristichoideae and Weddellinoideae.

In Tristichoideae, the flowers are terminal on pedicels subtended by bracts or a cupule, and the perianth comprises three tepals, basally fused

or nearly free (Fig. 1a). The cupule represents a cup shaped structure formed by leaf-like appendages that are syndesmically fused at their bases protecting the flower bud (Jäger-Zürn & Mathew, 2002). In the monotypic genus *Weddellina squamulosa* Tul. (Weddellinoideae), flowers arise terminally on bracteolate pedicels and bear 5 (sometimes 4 or 6) free tepals with imbricate aestivation (Fig. 1b). The blade-like tepals shared by Tristichoideae and Weddellinoideae are morphologically similar to those of Hypericaceae, the sister family to Podostemaceae. As such, the presence of a perianth with distinct tepals can be regarded as a symplesiomorphic trait, consistent with phylogenetic evidence that Tristichoideae is sister to the clade comprising Weddellinoideae and Podostemoideae (Ruhfel *et al.,* 2011; Koi *et al.,* 2012).

Spathella

The spathella is a distinctive, non-vascularized structure of uniform thickness, consisting of an epidermis and 2–4 layers of parenchyma cells that replaces the perianth and encloses the developing flower in Podostemoideae (Fig. 1c). Typically, it encloses a single flower, though an exception occurs in *Macarenia clavigera* P. Royen [= *Rhyncholacis clavigera* (P. Royen) B.R. Ruhfel & C.T. Philbrick], where 10–20 flowers develop within a single spathella (Cook & Rutishauser, 2007).

Spathella morphology is variable; shape of spathella can range from ellipsoid (*Polypleurum munnarense* Nagendran & Arekal) to ovoid (*Zeylanidium olivaceum* Engl., *Ctenobryum mangkonense* Koi & M. Kato) to obovoid

(*Zeylanidium lichenoides* Engl.). In some taxa (*Willisia arekaliana* Shivam. & Sadanand and *Willisia selaginoides* (Bedd.) Warm. ex Willis) the spathella develops a hard, cap-like, unequally bilobed tip (Fig. 2a). The surface of spathella also varies, is either smooth (*P. munnarense*) (Fig. 2b), papillate (*Z. lichenoides, Laosia ramosa* Koi, Won & M. Kato) (Fig. 2c), or hairy (*Rhyncholacis penicillata* Matthiesen, *Polypleurum chinense* B. Hua Chen & Miao Zhang). Additionally, in species such as *W. arekaliana* and *Podostemum weddellianum* (Tul.) Philbrick & Novelo, the epidermal cells of the spathella are impregnated with silica bodies (Fig. 2d).

As water levels in streams recede, pedicel elongation causes rupture of the spathella, an event that marks anthesis. The mode of rupture varies among species: it either ruptures irregularly at the apex like in *W. arekaliana* and *P. munnarense* or it may rupture along the longitudinal axis like in flowers of *Z. olivaceum* and *Z. lichenoides*. In most of the species the ruptured spathella persists till the fruit formation, and its residual shape often serves as a useful diagnostic character for some taxa (Cook, 1990; Cusset, 1992). The persisting spathella may assume diverse forms, it may be boat-shaped (*Z. olivaceum),* or may show an oblique (*Z lichenoides)* or nearly horizontal dehiscence line (*Cladopus nymanii* H. A. Möller*),* or a few apical teeth (*Oserya coulteriana* Tul.) (Rutishauser, 1997).

The two-lipped apex of the spathella, as seen in *Mourera, W. selaginoides,* and *W. arekaliana,* has been interpreted as homologous either to two

Fig. 1. Flowers in three subfamilies: **a**. *Dalzellia zeylanica* with thin tepals and three stamens (arrow heads); **b**. *Weddellina squamulosa* with pale tepals (arrowhead) (Photograph courtesy: Prof. M. Kato); **c**. *Zeylanidium lichenoides* with flowers in spathella (arrowhead) and flowers extruded from spathella (arrow).

prophylls (*Mourera*) or to two united bracts (*W. selaginoides, W. arekaliana*) (Rutishauser, 1997; Jäger-Zürn, 2005; Cook & Rutishauser, 2007; Khanduri *et al.,* 2014). In some Podostemoideae, such as *Rhyncholacis* Tul. and *Zeylanidium* Engl., the spathella appears during early development as an asymmetric collar that later matures into an obovoid structure with a minute lateral, anus-like opening (Rutishauser, 1997). However, molecular evidence from *Hydrobryum japonicum* Imamura suggests a different interpretation, indicating that the spathella is homologous to the tepals of Tristichoideae and Weddellinoideae, rather than to bracts (Katayama *et al.,* 2010).

The monotypic genus *Diamantina* Novelo, C.T. Philbrick & Irgang, is the only known member of Podostemoideae with some flowers lacking tubular spathella (Rutishauser *et al.,* 2005). In molecular phylogenies, *Diamantina* is resolved as sister to the remaining Podostemoideae (Koi *et al.,* 2012). The presence of open subtending bracts in place of tubular spathella in *Diamantina* may therefore represent a plesiomorphic condition, whereas the evolution of tubular spathella constitutes a synapomorphy of Podostemoideae (Rutishauser, 2016). In the absence of a perianth, the spathella plays a crucial protective role, shielding reproductive organs from the force of swiftly flowing water when submerged as well as from desiccation in air. Its intact sac-like form offers far more effective protection than the incomplete coverings of lobed or free tepals in other subfamilies (Kato *et al.,* 2022). This structural innovation is likely one of the key factors underlying the remarkable diversification of Podostemoideae into 47 genera and 294 species.

Androecium

Podostemoideae

The number of stamens in Podostemoideae is highly variable, ranging from a single stamen to several. In many neotropical genera such as *Apinagia* Tul., *Marathrum*, and *Rhyncholacis*, flowers bear a complete whorl of 7–12 stamens alternating with the tepals. In *Mourera fluviatilis* Aubl., the stamens are even more numerous (23–32), usually arranged in two whorls (Sobral-Leite *et al.,* 2011). Similar polyandrous condition occurs in other neotropical representatives *Apinagia, Rhyncholacis*, and *Mourera* (Rutishauser & Grubert, 1994). Flowers with such reduced perianth but conspicuously enlarged androecia have been described as 'brush-flowers,' owing to their resemblance to showy androecial displays in families such as Myrtaceae and Mimosoideae (Rutishauser & Grubert, 1994; Endress, 1996). By contrast, stamen number is markedly reduced in several other neotropical taxa—for example, 2–4 in *Lophogyne lacunose* (Tul.) C.T. Philbrick & C.P. Bove, 2–3 in *Castelnavia princeps* Tul. & Wedd., 2 in *Podostemum weddellianum*, and a single stamen in *Oserya coulteriana* (Van Royen, 1954).

Most paleotropical Podostemoideae bear dorsiventral and zygomorphic flowers in which the androecium is restricted to one side of the ovary, forming an andropodium (Fig. 2e). This structure is typically Y-shaped, resulting from the basal fusion of two filaments, with anthers borne on the forked ends, as seen in genera such as *Polypleurum* (Tul.) Warm. and *Zeylanidium*. In contrast, in certain African taxa such as *Inversodicraea botswana* Cheek, the two stamens remain free and are not fused into an andropodium (Cheek *et al.,* 2020). In other taxa, the androecium is further reduced to a single stamen, for example in *Podostemum barberi* Willis and *Saxicolella* Engl.

In addition to fertile stamens, filiform appendages—commonly referred to as "tepals"—are often present in the androecium. Developmental studies, however, have shown that these structures arise from androecial primordia, supporting their interpretation as staminodes (Sehgal *et al.,* 2009) (Fig. 2e). In both African and American species, an additional appendage may occur between the forked stamens at the apex of the andropodium, further indicating an androecial origin (Cook, 1996; Cook & Rutishauser, 2007). Such androecial

modifications exemplify a broader evolutionary trend in floral development, whereby stamens are either lost or transformed into staminodes following reductions in pollen production (Ronse Decraene & Smets, 2001). Rutishauser (1997) has suggested that the andropodium of Old World Podostemoideae was derived through the gradual loss of stamens on one side of the flower, leading to dorsiventral symmetry, reduction of stamen number to two, and subsequent basal fusion of filaments. Consequently, these filiform appendages should be best regarded as staminodes rather than true tepals.

In Podostemoideae, pollen is commonly released as dyads (Fig. 2f), a feature observed in all Australasian taxa, *Podostemum* from the New World, and several African members of the subfamily. Interestingly, *Lophogyne lacunosa* (Gardner) Bove & Philbrick, the sole representative of its genus endemic to southeastern Brazil, exhibits remarkable variation, producing pollen in monads, dyads, and tetrads within the same anther (Bove *et al.,* 2011). Dyad formation is exceedingly rare among angiosperms and represents an apomorphic condition in Podostemaceae, with a parallel occurrence only in the monocot family Scheuchzeriaceae (de Sá-Haiad *et al.,* 2010). Functionally, dyads may confer reproductive advantages in riverweeds by increasing the likelihood of multiple pollen grains reaching the stigma in single act, thereby enhancing pollination efficiency. This mechanism ensures rapid germination of sufficient number of pollen grains, and is particularly advantageous given the very short flowering period, characteristic of Podostemaceae (Khanduri *et al.,* 2014; Krishnan *et al.,* 2023).

Pollen grains of Podostemoideae are typically small, spheroidal to ellipsoidal, and tricolpate (Fig. 2f). Certain taxa, however, exhibit intraspecific variation, with additional tetracolpate and even pentacolpate grains reported, as in *O. coulteriana* (O'Neill *et al.,* 1997). Tricolpate pollen is widespread among advanced eudicots and is thought to have evolved independently on at least three occasions (Furness & Rudall, 2004). The presence of multiple apertures provides a selective advantage by enabling rapid pollen germination on the stigma, particularly under harsh or unpredictable ecological conditions (Furness & Rudall, 2004).

Across Podostemoideae, pollen maintains a consistent microechinate, granular exine, a feature considered convergent within the family (Furness, 2012). Nonetheless, spinulose pollen has been documented in several neotropical taxa, including *M. fluviatilis* and *Marathrum* spp. (Novelo & Philbrick 1993; O'Neill *et al.,* 1997). In *Polypleurum munnarense*, exine development reveals a granular infratectum (Krishnan *et al.,* 2023). The combination of dyad pollen and a dense granular infratectum in *P. munnarense* has been proposed to increase pollen bulk density and settling velocity, thereby improving stigma capture efficiency and reducing pollen loss in windy habitats (Krishnan *et al.,* 2023). Thus, the persistence of this archaic granular infratectum in Podostemaceae may represent an evolutionary adaptation ensuring reproductive success in challenging aquatic environments (Krishnan et al., 2023).

Tristichoideae and Weddellinoideae

In Tristichoideae, the number of stamens ranges from one as in *Tristicha*, to two or three in *Terniopsis*, and three in *Paradalzellia* Koi, P.L. Uniyal & M. Kato, *Dalzellia* Wight, *Indotristicha* P. Royen, *Indodalzellia* Koi & M. Kato, and *Cussetia* M. Kato (Cusset & Cusset, 1988; Kato *et al.,* 2003; Koi *et al.,* 2022). Pollen grains in these genera are spheroidal, pantoporate, with up to 12 pores, and are shed as monads (Fig. 2g). In contrast, *Weddellina* exhibits a variable number of stamens (5–25), producing prolate, tricolporate pollen grains about 15 μm in length, which are also released as monads (Jäger-Zürn, 1997).

Gynoecium

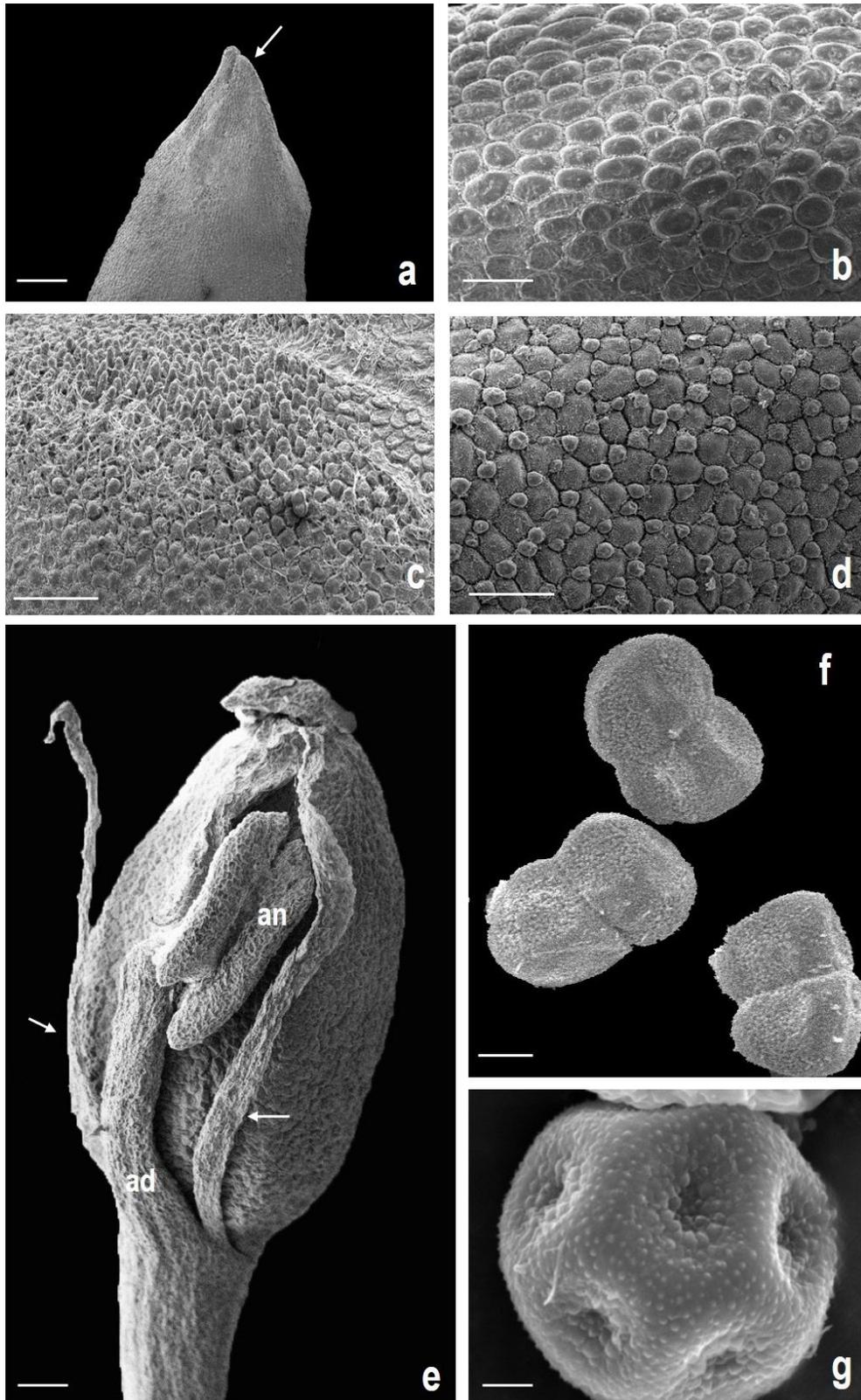A bicarpellate gynoecium is a defining feature of Podostemoideae. The ovary is typically bilocular,

Fig. 2. a. Beaked spathella in *Willisia arekaliana* Scale bar = 500 μm; **b**. Smooth-surfaced spathella in *Polypleurum munnarense* Scale bar = 100 μm; **c**. Papillate surface of spathella in *Zeylanidium lichenoides* Scale bar = 100 μm; **d**. Deposition of silica in the epidermal cells of spathella in *Willisia arekalianai* Scale bar = 50 μm; **e**. Flower of *Zeylanidium olivaceum* (spathella removed) staminodes (arrows), andropodium (ad) with anthers (an). Scale bar = 200 μm; **f**. Dyad, tricolpate pollen grain in in *Polypleurum munnarense* Scale bar = 10 μm; **g**. Monad, panporate pollen grain in *Dalzellia zeylanica* Scale bar = 2.7 μm (Photograph courtesy: Dr. Remya Krishnan).

with an inflated placenta tapering into a thin septum. Bilocular ovaries represent the plesiomorphic condition in the group, occurring in most of the New World members and all non-African Old World taxa, except *Hydrobryum micrantherum* (Royen) Cook and Rutish. (Cook and Rutishauser, 2007; Moline *et al.,* 2007). In contrast, unilocular ovaries are characteristic of several New World genera such as *Castelnavia* Tul. & Wedd. and *Apinagia,* and the African taxa. The locules may be equal or unequal (anisolobous); the latter is often associated with floral dorsiventrality and zygomorphy, as seen in many Asian podostemoids, where the upper locule is usually larger than the lower (Khanduri *et al.,* 2014).

With few exceptions, the ovary bears two stigmas, while the style is usually inconspicuous; in some taxa, the stigma lobes are basally united into a short stylar region (e.g., *Marathrum schiedeanum* Cham.; Cusset, 1992). Stigma morphology is highly variable: a single semi-globose stigma

occurs in the African genus *Angolaea* Wedd. (Cook, 1990); multilobed stigmas are seen in *Zeylanidium maheshwarii* C.J. Mathew & V.K. Satheesh and *Crenias weddelliana* (Tul.) C.D.K. Cook & Rutish. (Cook, 1990; Mathew & Satheesh, 1997); while stigmatic lobes may be equal (*Hydrobryopsis sessilis* Engl.) or unequal (*Podostemum subulatum* Gardner). In several African genera (*Angolaea, Leiothylax* Warm.,) and the Indian *Z. maheshwarii,* a gynophore elevates the gynoecium above other floral organs, facilitating self-pollination (Krishnan *et al.,* 2019).

By contrast, Tristichoideae possess a tricarpellate, syncarpous gynoecium with a trilocular, multi-ovulate ovary surmounted by three linear stigmas. Weddellinoideae have a bilocular ovary with a single globular, papillose stigma.

Thus, floral morphology provides clear distinctions among the three subfamilies (Table 1, Fig. 1). Flowers of Tristichoideae and Weddellinoideae

Table 1. A comparison of reproductive features among the three subfamilies of Podostemaceae (compiled from Mohan Ram & Sehgal, 1992; Cook and Rutishauser, 2007; Kato *et al.,* 2022).

Sl. No.	Character	Podostemoideae	Tristichoideae	Weddellinoideae
1	Flower	Dimerous	Trimerous	Pentamerous
2	Floral symmetry	Actinomorphic or zygomorphic	Actinomorphic	Actinomorphic
3	Spathella	Present	Absent	Absent
4	Perianth	Absent	Fused into three-lobed 'calyx'	Four to six (usually five) free tepals
5	Stamen	1– 44 (1 or 2 in Asian and African taxa, many in neotropical taxa)	Three	5 – 25 (sometimes one or two)
6	Staminodes	Present	Absent	Absent
7	Pollen	Tricolporate/ Tricolpate, rarely tetra- or pentacolpate	Pantoporate	Tricolporate
8	Pollen units	Dyads or Monads	Monads	Monads
9	Gynoecium	Bicarpellary and syncarpous	Tricarpellary and syncarpous	Bicarpellary and syncarpous
10	Ovary	Bilocular or unilocular	Trilocular	Bilocular
11	Stigma	Mostly two lobed	Three lobed	One globular, papillose stigma

are actinomorphic, whereas those of most Podostemoideae are zygomorphic. Tristichoideae flowers are trimerous, with three fused tepals, 1–3 stamens, and a trilocular ovary with three stigmas. Weddellinoideae flowers bear 5 (rarely 4 or 6) free tepals, 5–25 stamens, and a bilocular ovary with one stigma. Podostemoideae flowers are unique in having a spathella, none to many tepals, 1–many stamens, and a bi- or unilocular ovary with one or two stigmas

Pollination ecology

Pollination systems in the Podostemaceae have received relatively limited attention, especially considering the size and diversity of the group. Existing studies on the pollination biology of the family indicate that most species predominantly rely on self-pollination (more specifically, spontaneous autogamy), often employing distinct and specialized mechanisms (Khosla *et al.,* 2000, 2001; Gupta & Seghal, 2009; Seghal *et al.,* 2009, 2010; Khanduri *et al.,* 2014; Krishnan *et al.,* 2019; Khanduri *et al.,* 2024). While self-pollination appears to be widespread within the family, reports also suggest that other pollination vectors—such as wind, small insects, bees, beetles, and flies may contribute to cross-pollination in certain species like *Apinagia richardiana* (Tul.) P. Royen (Sobral-Leite 2009); *A. riedelii* (Bong.) Tul. (Sobral-Leite 2013); *M. fluviatilis* Aubl. (Sobral-Leite *et al.,* 2011); *Lophogyne royenella* C. P. Bove & C. T. Philbrick (as *Lophogyne capillacea* (Tul.) C.T. Philbrick & C. P. Bove, *L. fimbrifolia* (P. Royen) C. T. Philbrick & C. P. Bove, *Marathrum capillaceum* Pulle, and *M. aspera* Tul. (da Silva-Batista, 2019). Considering the involvement of pollinators in these plants and self-compatible nature of these plants in general, the extent of self:cross pollination within a flower is not known yet.

Podostemoideae

Like the other podostemads, flowering in neotropical Podostemoideae is stimulated in dry seasons, when the water level drops. Besides, floral features like the absence of nectar; a reduced perianth; exserted stamens and pistils; numerous dry, readily dispersed, tiny pollen grains; populations with synchronous, abundant flowering suggests that the floral characteristics of neotropical species could facilitate pollination by wind (Rutishauser and Huber, 1991; Rutishauser, 1997; Philbrick & Novelo 1998; Okada and Kato, 2002; Sobral-Leite *et al.,* 2011; da Silva-Batista *et al.,* 2021). However, this premise has only been empirically tested in species like *Marathrum foeniculaceum* Bonpl. (cited as *Marathrum rubrum* Novelo & C.T. Philbrick by Philbrick & Novelo, 1997; Pérez-Pacheco *et al.,* 2024), *M. fluviatilis* Aubl. (Sobral-Leite *et al.,* 2011) and *L. lacunosa* (da Silva-Batista *et al.,* 2020). It was seen that all these species are not obligately allogamous and anemophilous. All these species undergo self-pollination in addition to anemophily. *Lophogyne lacunosa* is very interesting in possessing several strategies for reproductive assurance including self-pollination, wind-pollination and apomixis. In addition, it also produces parthenocarpic (seedless) fruits in natural conditions (da Silva-Batista *et al.,* 2020).

Neotropical species have other floral characteristics that contrast with those typical of anemophilous species especially from the genera *Apinagia, Mourera, Rhyncholacis* and *Marathrum* (Rutishauser, 1997; Tavares, 1997; Okada and Kato, 2002; Sobral-Leite *et al.,* 2011; Sobral-Leite, 2013; Pérez-Pacheco *et al.,* 2024). For instance, presence of showy and numerous stamens, brightly colored filaments and pedicels, presence of pollen grains with microechinate exine, bilobed and showy papillate stigma unlike the feathery stigmas typical of wind-pollinated species, or numerous ovules, floral odour and visitor insects. There are many records of bees visiting flowers of Neotropical species, suggesting a possible cross-pollination by biotic vectors. Species of *Trigona, Tetragona, Apis* and *Melipona* (Apidae) are frequent visitors of Neotropical Podostemaceae (Gessner & Hammer, 1962; Tavares, 1997; Okada & Kato, 2002; Sobral-Leite *et al.,* 2011; Sobral-Leite, 2013; Pérez-Pacheco *et al.,* 2024). In *M. fluviatilis,* a species found in the

Amazon and northeastern Brazil, *Augochlora* sp., *Augochloropsis* sp. and *T. spinipes* are known to be the effective pollinators. Brightly colored pedicels, filaments and emission of sweet odor in *M. fluviatilis* are attributes that attract bees. It was also shown that emasculation of *M. fluviatilis* flowers led to a decrease in seed-set which is due to a loss of attractiveness to pollinator bees, as the stamens are the most conspicuous floral parts. However, the species is not solely dependent on biotic transport of pollen among flowers and also undertakes self-pollination towards the end of anthesis. Similar floral morphological characteristics have also been observed in another neotropical species visited by bees, *Marathrum rubrum* (Pérez-Pacheco *et al.,* 2024). This species attracts pollinators by producing pollen grains in large numbers and emitting floral scents. The study also documented the presence of osmophores and idioblasts located in various floral structures that emit floral scent. All these reports suggest that neotropical podostemads do not have any adaptations to specific visitors.

Genus *Podostemum* is a unique taxon with species occurring both in neotropical and paleotropical regions. It is characterized by asepalous, apetalous flowers enveloped within a spathella. Thus, new world species of *Podostemum* are unlike other neotropical species in terms of floral size and morphology. Pre-anthesis cleistogamy (pollination before the flower bud emerges above the level of water) has been reported from two Neotropical species of the genus, *Podostemum*, (*P. ceratophyllum* Michx., Philbrick, 1984 and *P. weddellianum*, Silva-Batista *et al.,* 2020).

Among the paleotropical species, reproductive biology is known from only the Indian species which include *Polypleurum stylosum* (Wight) J.B.Hall (Khosla *et al.,* 2000), *Griffithella hookeriana* (Tul.) Warm. (Khosla *et al.,* 2001), *Hydrobryopsis sessilis* (Sehgal *et al.,* 2009), *Willisia arekaliana* (Khanduri *et al.,* 2014), *Zeylanidium maheshwarii* (Krishnan *et al.,* 2019), *Podostemum subulatum* (Khanduri *et al.,* 2024).

The flowers in paleotropical podostemads are much smaller in size than to their New World counterparts. Flowers lack perianth, possess one or two stamens per flower which are restricted to one side of the ovary in an andropodium, and dyad pollen grains. The floral attributes that attract pollinators are absent. Neotropical species possess adaptations for autonomous self-pollination such as: proximity between dehisced anthers and receptive stigmas, overlapping male and female reproductive phases, introrsely dehiscing anthers and elongation of filament and/or andropodium (Khosla *et al.,* 2000; Sehgal *et al.,* 2009; Khanduri *et al.,* 2014; Krishnan *et al.,* 2019; Khanduri *et al.,* 2024). However, each species has evolved a distinct strategy for self-pollination. Self-pollination above water facilitated by the elevation of flowers by rapid elongation of the pedicels occurs in species like *P. stylosum* (Khosla *et al.,* 2000). Self-pollination at the water-air interface by partial emergence from the spathella is seen in sessile flowers of *W. arekaliana* (Khanduri *et al.,* 2014). Self-pollination under water within the spathella termed as "pre-anthesis cleistogamy" is seen in *H. sessilis* and *P. subulatum* (Sehgal *et al.,* 2009; Khanduri *et al.,* 2024). The occurrence of diverse self-pollination mechanisms within similar ecological settings illustrates how functional aspects of floral biology contribute to reproductive assurance. So far, there has been no report of insect pollination in paleotropical species. Although some water fleas are seen around the plants it is presumed, they use the thallus either for food, shelter, protection from predators or for capturing preys rather than effect pollination. The role of wind, however, has not been excluded completely as controlled pollinations experiments show that both self- and cross-pollen germinate on the stigma and there is a possibility that cross-pollination (xenogamy) may also occur to a limited extent (Khosla *et al.,* 2000). However, this is restricted to species in which pollination takes place above the water level.

Reduction in the size and number of reproductive structures coupled with zygomorphy is a

Table 2. Modes of pollination reported in Podostemaceae

Sl. No.	Taxon	Flower	Mode of pollination	Breeding system	Reference
Podostemoideae					
1	*Apinagia richardiana* (Tul.) P.Royen	Solitary or in clusters, Actinomorphic, multi-stemonous	Melittophily	Allogamy	Sobral-Leite, 2009
2	*Apinagia riedelii* Warm.	Flowers in inflorescence, Actinomorphic, multi-stemonous	Melittophily	Allogamy	Sobral-Leite, 2013
3	*Griffithella hookeriana* (Tul.) Warm.	Solitary, Zygomorphic	Self-pollination under water before anthesis (pre-anthesis cleistogamy)	Obligate autogamy	Khosla *et al.,* 2001
4	*Hydrobryopsis sessilis* Engl.	Solitary, Zygomorphic	Self-pollination under water before anthesis (pre-anthesis cleistogamy)	Obligate autogamy	Sehgal *et al.,* 2009
5	*Lophogyne lacunosa* (Gardner) C.P.Bove & C.T.Philbrick	Solitary, Zygomorphic	Self-pollination, wind pollination, and apomixis.	Mixed	Da Silva Batista *et al.,* 2019
6	*Marathrum rubrum* Novelo & C.T.Philbrick	Solitary, actinomorphic, seven-nine stamens	Ambophily and self-pollination	Mixed	Pérez-Pacheco *et al.,* 2024
7	*Mourera fluviatilis* Aubl.	Flowers in inflorescence, actinomorphic, multi-stemonous	Cross-pollination by bees followed by self-pollination at the end of anthesis	Mixed	Sobral Leite *et al.,* 2011
8	*Podostemum subulatum* Gardner	2-8 axillary flowers, Zygomorphic	Self-pollination under water before anthesis (pre-anthesis cleistogamy)	Obligate autogamy	Khanduri *et al.,* 2024
9	*Podostemum weddellianum* (Tul.) C.T.Philbrick & Novelo	Solitary, Zygomorphic	Self-pollination before anthesis (pre-anthesis cleistogamy) and after anthesis	Facultative autogamy	da Silva Batista *et al.,* 2019
10	*Polypleurum stylosum* (Wight) J.B.Hall	Solitary, Zygomorphic	Self-pollination above water level	Facultative Autogamy	Khosla *et al.,* 2000
11	*Willisia arekaliana* Shivam. & Sadanand	Solitary, Zygomorphic	Self-pollination at air-water interface	Obligate autogamy	Khanduri *et al.,* 2014

Sl. No.	Taxon	Flower	Mode of pollination	Breeding system	Reference
12	*Zeylanidium maheshwarii* C.J.Mathew & V.K.Satheesh	Solitary, Zygomorphic	Self-pollination above water-level	Autogamy	Krishnan *et al.,* 2019
			Tristichoideae		
13	*Indotristicha ramosissima* (Wight) P.Royen	Solitary, actinomorphic	Self-pollination above water level	Facultative Autogamy	Khosla Gupta & Sehgal, 2009
14	*Dalzellia ceylanica* (Gardner) Wight	Solitary, actinomorphic	Self-pollination above water level	Facultative Autogamy	Sehgal *et al.* 2010
15	*Tristicha trifaria* Spreng.	Solitary, actinomorphic	Self-pollination above water level	Obligate Autogamy	da Silva Batista *et al.,* 2019
			Weddellinoideae		
16	*Weddellina squamulosa* Tul.	Solitary, actinomorphic	Melittophily and self-pollination.	Mixed	da Silva Batista *et al.,* 2021

characteristic of the Old World Podostemoideae (Willis, 1902). Zygomorphy is usually an attribute of entomophilous flowers and is of advantage to them, but flowers of the Old World Podostemoideae are very small and are not visited by insects at least not for pollen scavenging. Therefore, the extreme zygomorphy in the Old World Podostemoideae in general can be attributed to a tendency towards autogamy. This trend of actinomorphy/allogamy to zygomorphy/autogamy can be exemplified by entomophilous/actinomorphic flowers of Neotropical Podostemoideae to self-pollinated/zygomorphic flowers of Old World Podostemoideae.

Tristichoideae

Within Tristichoideae, reproductive biological studies have been accomplished in only three genera; *Indotristicha*, *Dalzellia* and *Tristicha* (Gupta & Sehgal, 2009; Sehgal *et al.,* 2010; Da Silva-Batista *et al.,* 2020). All the species show autogamy under aerial conditions. Pollination above water is facilitated both by seasonal drop in water level of the river and by elongation of the pedicels to elevate flowers above water. Both the species show rapid increase in the length of pedicel (approx. up

to 2 cm). Also, elongation of the filaments from the time of anthesis (from 0.7 cm to 2.0 cm in *I. ramosissima*, 0.2 cm to 1.5 cm in *D. zeylanica* and 0.5 cm to 1.22 cm in *T. trifaria*) to bring the anthers above the stigmas such that the pollen can readily be deposited onto stigmas making self-pollination almost certain. There are no published reports of pollination biology or breeding system of other genera within Tristichoideae. All the genera have small typical Tristichoid flowers; bisexual, trimerous flowers, with up to 3 stamens and might therefore be inferred to be self-pollinated.

Weddellinoideae

The flowers of *Weddellina squamulosa*, possess five blade-like tepals, a varying number of stamens (5–25), monad pollen grains, a bicarpellate pistil borne on a sparsely-bracteolate pedicel (Furness 2012). The flowers have pigmented floral and associated structures like pink flowering shoot and bracts, light-pink tepals and numerous purple or dark-pink anthers (da Silva Batista *et al.,* 2021). Also, the flowers are produced in large numbers and have fragrance but do not produce nectar and provide only pollen as reward. All these characters indicate

melittophily which was speculated by Grubert (1974). Some Halictid bees (*Augochloropsis* sp. and *Dialictus* sp.) were confirmed to be the pollinators of *W. squamulosa* flowers by experimental observations (Da Silva Batista *et al.,* 2021). Species was also shown to undergo elongation of filaments which moves the whorl of stamens, away from the stigma in the first two hours of anthesis, causing cross-pollination followed by return of stamens to the center of the flower and touching stigmas causing delayed selfing. The species also has papillose stigmas with a copious mucilaginous secretion indicating a wet stigma.

Evolutionary implications

Podostemaceae is a member of the clusioid clade within the order Malpighiales, which also includes Ochnaceae, Bonnetiaceae, Calophyllaceae, Clusiaceae, and Hypericaceae (Ruhfel *et al.,* 2011; APG IV, 2016). Within this clade, Podostemaceae is unique as the only fully aquatic family, while the others are terrestrial. The specialized habitats of Podostemaceae, such as rapids and waterfalls, impose strong selective pressures and are generally inhospitable to pollinators and cross-pollination. Accordingly, the floral traits of Podostemaceae are markedly distinct from those of other clusioid families. Whereas most clusioid families exhibit a wide range of floral adaptations promoting cross-pollination—offering rewards such as nectar, pollen, and floral resins to diverse pollinator groups—podostemads provide only pollen (Bittrich *et al.,* 2006; Amaral *et al.,* 2013; Costa, 2016; Martarello *et al.,* 2024), resulting in visitation by a limited set of potential pollinators (Cook & Rutishauser, 2007). Aquatic families within otherwise terrestrial orders are thought to have evolved from emergent ancestors (Barrett & Graham, 2000). In Podostemaceae, vegetative and reproductive traits were probably acquired early, through sequential adaptations to the demands of their extreme habitats, eventually enabling growth in waterfalls and rapids (Kato *et al.,* 2022). Pollination mode in Podostemaceae

ranges from entomophily, anemophily, to self-pollination (Table 2). Although observations are lacking for several genera, self-pollination is seen in the most basally diverged Tristichoideae, entomophily followed by delayed self-pollination in Weddellinoideae and self-pollination observed in almost all main clades in in Podostemoideae. Possession of remnants of floral structures devoted to outcrossing suggests that self-pollination in Podostemaceae is a relatively recent apomorphy derived from outcrossing ancestors.

The transition from outcrossing to selfing is considered the most common evolutionary transition in flowering plants, having arisen repeatedly in many independent lineages (Stebbins, 1974). Two selective forces are thought to drive this transition: the transmission advantage of selfing over outcrossing genotypes and the reproductive assurance value of selfing in poor pollination environments (Goodwillie *et al.,* 2005). In the absence of asexual reproductive strategies and challenging ecological conditions, mechanisms ensuring reproductive assurance are especially critical for Podostemaceae. Consequently, traits promoting autonomous self-pollination have likely evolved to secure seed-set and improved colonization ability under these extreme environments. Floral adaptations promoting selfing across all lineages in Podostemaceae include: loss of nectar or floral rewards, reduced spatial separation of reproductive organs and synchrony of male and female function. In addition, other apomorphic states appeared in part in lineages of Podostemaceae and drove the diversification of the family, in particular subfamily Podostemoideae. Characteristics like evolution of spathella, dyad pollen grains, origin of zygomorphic dorsiventral flowers may contribute to the additional minor adaptations for self-pollination and great diversity in the Podostemoideae. Studies of the pollination biology of Podostemoideae, which contains approx. 280 (90%) species of the family, may be worthwhile to help understand the great diversity in this subfamily.

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