Podostemaceae

Podostemaceae L. Richard ex C. Agardh, Aphor. Bot.: 125 (1822), nom. cons.
Tristichaceae J.C. Willis (1915).

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Annual or perennial, aquatic herbs, often bizarre in form, sometimes resembling lichens, bryophytes, seaweeds, or unlike any other plants; haptophytes, attached by adhesive hairs to rock or other hard objects in flowing freshwater, mostly in rapids and waterfalls; roots usually photosynthetic, creeping or partly floating, thread-like, ribbon-shaped, crustose (foliose), sometimes short-lived or absent. Shoots nearly always arising as endogenous buds from roots; stems reduced or elongate, simple or branched, sometimes dimorphic, occasionally only present when flowering. Photosynthesis takes place under water, flowers or even separate floral shoots develop as the water level drops, the vegetative shoots or leaves often shed as plants become exposed. Phyllotaxis variable, in Podostemoideae usually distichous. Leaves borne on elongate stems or arising from prostrate, often disk-like stems, extremely variable in size and shape, from scale-like to well developed and compound; sheaths single or, in many Podostemoideae, double; sheath lobes sometimes elongated into stipule-like appendages; leaf blades stalked or sessile, entire, lobed or dissected; blade lobes or segments often bearing photosynthetic filaments and/or additional hairs; ultimate leaf segments filiform, linear or spathulate. Flowers bisexual, actinomorphic or zygomorphic, solitary, in clusters or in raceme- or cyme-like inflorescences; flower buds naked in Weddellinoideae and some Tristichoideae, surrounded by a cupula (a collar-like vascularised cup) in some Tristichoideae, or completely enclosed in a spathella (a tubular or sack-like cover) in Podostemoideae; spathellas mostly enclosing a single sessile or pedicellate flower; pedicels often elongating in fruit. Anthesis takes place in air or flowers cleistogamous under water. Perianth of 1 complete or incomplete whorl of tepals, often confined to one side of the flower; tepals in Tristichoideae and Weddellinoideae large, 5 or rarely 4 or 6, imbricate and sepal-like; tepals in Podostemoideae small, 2–20, linear or subulate, usually alternating with stamens, in flowers with only 2 basally fused stamens occasionally an additional tepal borne at top of andropodium (common stalk); stamens 1–40, in 1 or 2 complete whorls, or in 1 incomplete whorl, or confined to one side of flower and consisting of 1–3 free stamens or a Y-shaped structure consisting of an andropodium carrying 2 stamens; filaments, when in whorls, mostly free or, in *Tulasneantha*, their bases united to form an androecial tube; anthers dehiscing longitudinally by slits, introrsely to latrorsely or rarely extrorsely; pollen shed in monads, dyads or (rarely) tetrads, tricolporate in Weddellinoideae, tricolpate to pentacolpate in Podostemoideae, pantoporate with up to 16 pores in Tristichoideae; ovary superior, 2- or 3-locular or 1-locular in some Podostemoideae; ovules axile, anatropous, bitegmic, tenuinucellate. Fruit a capsule, smooth or ribbed, with 2 or 3, equal or unequal valves, sometimes one or more persisting; stigmas 1–3, variable in shape and size. Seeds 2 to very numerous (over 2,000); seed coat usually mucilaginous and sticky; endosperm 0; embryo straight, with 2 cotyledons and a suspensor.

The family consists of 49 genera, of which 26 (53%) are monotypic or nearly so (some have two doubtfully distinct species) and about 280 species. It is distributed worldwide in tropical and warm regions, extending into temperate eastern North America and temperate East Asia. Most of the species are endemic to small geographical areas; only one, *Tristicha trifaria*, is widespread and occurs in the Old and New Worlds.

Vegetative Morphology. The interpretation of the vegetative body is controversial. Many Podostemaceae have a flattened photosynthetic body which adheres to a hard substrate. It has been called a 'thallus' because the conventional demarcation into stem, leaf and root is usually not obvious (Cario 1881; Willis 1902), and various botanists have denied or doubted the homology of this vegetative body with stems (caulomes),

leaves (phyllomes) and roots of other angiosperms (G. Cusset 1974; Cusset and Cusset 1988; C. Cusset 1992; Mohan Ram and Sehgal 1992, 2001; Schnell 1994, 1998; Khosla et al. 2000; Ota et al. 2001; Sehgal et al. 2002). These botanists consider the vegetative body of all (or most) Podostemaceae represents a unique architectural type. However, for convenience, we adopt the classical root-shoot model (CRS model) with its structural categories roots, shoots (including stems and leaves) as used by Warming (e.g. 1881), Goebel (1933), Rauh (1937), Troll (1941), Jäger-Zürn (e.g. 1970, 2000c), Rutishauser and Huber (1991) and Rutishauser (1997). We avoid the term 'thallus'. We use the term 'root' for cylindrical to flattened photosynthetic structures when endogenous shoot buds are developed but no exogenous leaves. The term 'stem' is applied to a cylindrical or flattened photosynthetic body which develops exogenous leaves. For example, the prostrate and crustose body of *Hydrobryum* (Fig. 104C) and *Zeylanidium olivaceum* (Fig. 124D, F), which lacks exogenous leaves, is described as a root (Jäger-Zürn 2000b; Rutishauser and Moline 2005). The prostrate and often star-shaped body of *Dalzellia zeylanica* is described as a flattened stem or branch system because it bears exogenous scales which are often interpreted as leaves (Jäger-Zürn 1995; Imaichi et al. 2004).

Podostemaceae show an amazing diversity of root types. Usually, the roots are persistent with long-lasting apical growth, bearing root-borne shoots and fixed to the hard substrate by adhesive hairs (Fig. 107A). They vary from thread-like (cylindrical) to ribbon-like and further to crustose (i.e. foliose, disk-like). The roots give rise to endogenous shoot buds, either from the flanks or in crustose roots also from the upper surface (Fig. 104C). Cylindrical to narrowly ribbon-like roots of Podostemaceae are normally provided with an asymmetric cap which resembles the calyptra of a typical root (Fig. 104A; Koi and Kato 2003). Broad ribbons and crustose (i.e. foliose, disk-like) roots often lack an obvious cap. Lateral roots of ribbon-like roots arise endogenously or exogenously (Fig. 104B), or show a mosaic pattern of endogenous and exogenous formation (e.g. *Cladopus* spp., Koi and Kato 2003). Crustose roots are found especially in Asian Podostemoideae (e.g. *Hydrobryum*, *Zeylanidium olivaceum*) and African Podostemoideae (e.g. *Dicraeanthus*, *Ledermanniella* spp.; Cusset 1984). The crustose root of *Hydrobryum* contains a network of nonvascular strands (Ota et al. 2001). The crustose roots of *Hydrobryum* grow with a marginal meristem giving rise to exogenous lobes. The margin of these flat roots are fringed by a protective tissue which may be considered as a rudimentary cap (Suzuki et al. 2002). A progressive elaboration of the root is most obvious in Asian and Australian Podostemoideae where it is accompanied by gradual reduction of the cap (calyptra) and decrease in size of the root-borne leafy shoots (Willis 1902; Jäger-Zürn 2000a; Suzuki et al. 2002). Crustose roots have evolved at least three times in Podostemaceae, twice in Asian podostemoids and at least once in African members (Hiyama et al. 2002; Kita and Kato 2004b; Moline et al. 2007).

In several genera the roots are insufficiently documented. There are a few species which lack obvious roots, e.g. *Castelnavia princeps*, *Dalzellia zeylanica*, *Mourera fluviatilis* and *Rhyncholacis carinata*, although other species in the same genera are clearly provided with roots (Warming 1899; Rutishauser and Grubert 1994; Mathew et al. 2001). Holdfasts (haptera in earlier literature) are claw-like organs superficially resembling the attachment organs of brown algae such as *Fucus*. They stick the plants to the solid substratum. They may be branched (e.g. *Polypleurum* spp.) or finger-like (e.g. *Saxicolella submersa*, Ameka et al. 2002). They arise as exogenous (e.g. *Podostemum ceratophyllum*) or endogenous outgrowths (e.g. *Indotristicha ramosissima*) of the root. Holdfasts may also arise as exogenous outgrowths from the base of leaves and shoots.

All Podostemaceae investigated to date have dicotyledonous seedlings. The shoots of most arise as endogenous buds from hypocotyl-borne outgrowths (roots) which soon replace the short-lived seedling axis (Mohan Ram and Sehgal 1997; Sehgal et al. 2002). Seedling establishment by plumular activity seems to be the exception, rather than the rule; it is found in a few New World Podostemaceae such as *Apinagia multibranchiata* and *Mourera fluviatilis* (Grubert 1976; Rutishauser and Grubert 2000). More seedling features are described below under Seedlings and Life Cycle.

Many African and American members of the Podostemoideae form elongate and branched shoots over 80 cm long (e.g. *Ledermanniella bowlingii*, Ameka et al. 2003), whereas a reduction in size of the root-borne shoots to 1 cm or less long and often unbranched is typical for most Podostemoideae in Asia. The longest shoots formed by Asian podostemads are those of *Indotristicha*