# Podostemaceae—the strange family of aquatic angiosperms

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Podostemaceae is a unique family of aquatic angiosperms. The vegetative body of the podostemads is represented by a thallus resembling that of an alga, lichen or a bryophyte, and lacking the conventional demarcation into stem, leaf and root. The podostemads invariably inhabit gushing mountain streams or falls and generally grow attached to rocks. They lack aerenchyma. Flower buds are initiated while submerged, but flowering and fruit development occurs when the water level subsides and the plants become exposed. Taxonomists believe that podostemads have affinities with Crassulaceae, Saxifragaceae and Hydrostachydaceae. Podostemaceae are termed an embryological family owing to the lack of antipodals, triple fusion, endosperm, the prevalence of single fertilization, and the presence of a pseudo-embryo sac. The wide range of phenotypic plasticity, morphological nature of the thallus as understood by developmental studies using in vitro cultures, and embryological features of the family are discussed. The origin, adaptation and affinities with closely related families have also been examined.

**Key-words**—Taxonomy, Podostemaceae, Aquatic angiosperms, Embryology, Polymorphism.

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**सारांश**

**जलीय आवृतबीजीयों का विचित्र कुल – पोडोस्टीमेसी**

एच० वाई० मोहनराम एवं अनिता सहगल

पोडोस्टीमेसी जलीय आवृतबीजीयों का एक विचित्र कुल है। इस कुल के पौधों की वर्धीकाय शैवाल, लाइकेन अथवा एक ब्रायोफाइटी पौधे के सूकाय से समानता प्रदर्शित करती है तथा इनमें तना, पत्ती एवं जड़ का स्पष्ट विभेद नहीं होता। इस कुल के पौधे स्थायी रूप से धाराप्रवाही पर्वती झरनों में पाये जाते हैं तथा सामान्यतः चट्टानों से चिपके रहते हैं। इन पौधों में एरनकाइमा अनुपस्थित होता है। जब ये पानी में डूबे होते हैं तभी पुष्प-कली बनना प्रारम्भ होती है परन्तु फल एवं बीज तभी बनते हैं जब पानी का स्तर कम हो जाता है तथा पौधा दिखाई देने लगता है। वर्गिकीविदों का मत है कि ये पोडोस्टीमेडियन पौधे क्रेसूलेसी, सेक्सीफ्रेगेसी एवं हाइड्रोस्टेकिडेसी नामक कुलों से सजातीयता प्रदर्शित करते हैं। पोडोस्टीमेसी कुल एक ऐसा कुल है जिसमें प्रतिव्यासांत, त्रिसंलयन एवं भ्रूणपोष नहीं होते, एकल निषेचन होता है तथा आभासी-भ्रूण कोष पाया जाता है। सूकाय की आकारिकीय प्रकृति आदि तथा भ्रूणीय लक्षणों आदि के विषय में भी विवेचना की गई है। इसके अतिरिक्त घनिष्ठ सम्बद्ध कुलों से इसकी उत्पत्ति, अनुकूलनता तथा सजातीयता की भी समीक्षा की गई है।

EVOLUTIONISTS believe that diversity and unity are twin themes that characterize the living world. Evolution is considered as a means to reconcile these contrasting, mutually exclusive phenomena (Savage, 1965). Two results of evolution are adaptation and specialization. Adaptation refers to efficient interaction with environment and specialization means occupying restricted niches. The Podostemaceae present a challenging task to study these phenomena.

The podostemads grow attached to waterworn rocks, boulders and wood pieces located under waterfalls and in rapidly flowing streams where only certain mosses and algae survive. The family is represented by 46 genera and 260 species (Cook, 1974). However, Nagendran (1975) lists 49 genera and 240 species. The members are restricted to tropical and subtropical regions of the world. Twenty species are recorded from India, of which 18 are endemic. Most of these are concentrated in the Western Ghats, whereas a few occur in Meghalaya,

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Madhya Pradesh, Orissa, Maharashtra and Goa (Vartak & Bhadbade, 1973). The populations of podostemads, though localized, are dense indicating their relative fitness.

Willis (1902) described Podostemaceae as having "most varied morphological structure". Arber (1920) in her monumental work on water plants referred to this group as "peculiar and anomalous". Sculthorpe (1967) has remarked: "There is surely no stranger and more provocative family of angiosperms than Podostemaceae". A combination of characteristics that make them an unusual family among angiosperms are: their thalloid growth habit, perplexing polymorphism, marked structural reductionism, presence of unique embryological features, submersed vegetative and emersed reproductive phase.

Taxonomical and embryological accounts on Podostemaceae are available (Tulasne, 1852; Maheshwari, 1955; Chopra & Mukkada, 1966; Takhtajan, 1966; Battaglia, 1971; Nagendran, 1975; Cronquist, 1988). Nevertheless, the amount of unknown information is vast, probably because of the obscurity and inaccessibility of material for study. Swollen rivers dissuade botanists to make field investigations, especially during the period of seedling establishment in nature. According to Pannier (1960) "the reason for the lack of research on this interesting group of plants is undoubtedly due to impossibility of maintaining them alive out of their natural habitat for any period of time".

## SEED GERMINATION, THALLUS DEVELOPMENT AND MORPHOLOGY AND FLOWERING

It is difficult to collect seedlings in nature and unless a comparative account of germination in the family is carried out, the true nature of the plant body will remain enigmatic. Nagendran (1975) was the first to germinate the seeds of nine taxa under laboratory conditions. However, he was unable to keep the seedlings growing beyond a few days.

Our research group at the University of Delhi has successfully developed a simple and reproducible technique of raising podostemads from seeds to mature plants in axenic cultures (Vidyashankari, 1988a, b; Vidyashankari & Mohan Ram, 1987; Mohan Ram & Sehgal, unpublished). It is envisaged to investigate the ultrastructure and development of the different phases of their life cycle. In the taxa investigated by us, the plant body is thalloid and bewilderingly polymorphic. It is star-like in *Dalzellia zeylanica*, cup- or funnel-like in *Griffithella hookeriana*, ribbon-shaped in *Polypleurum stylosum*, crustaceous in *Hydrobryopsis sessilis* and thread-like in *Indotristicha ramosissima*. The ability of these plants to develop into exceptional forms can perhaps be attributed to the absence of a rigid skeletal system (Sculthorpe, 1967). Podostemads have no conventional distinction into stem, root and leaf. The thallus bears gum-secreting rhizoids which cement it to the substratum. The vertical section of a thallus of *Griffithella* shows no vasculature. The thallus cells contain copious amount of silica granules, the significance of which is not known. Aerenchyma, so characteristic of the hydrophytes is absent in the Podostemaceae. The probable reason for this could be the firm attachment of thalli to the substratum which obviates the necessity for buoyancy.

Podostemads start their annual life cycle with the onset of monsoon. Their seeds are tiny. Vidyashankari (1988a) reported that 1,236,100 seeds of *Griffithella hookeriana* weigh one gram. The number of seeds per fruit varies from 2-8 in *Farmeria* (Arekal & Nagendran, 1974) to 240 ± 25 in *Polypleurum stylosum* (Mohan Ram & Sehgal, unpublished).

In the taxa investigated by us, i.e., *Dalzellia zeylanica, Griffithella hookeriana* (Vidyashankari, 1988a, b), *Hydrobryopsis sessilis, Indotristicha ramosissima, Polypleurum stylosum, Zeylanidium lichenoides*, the embryo shows two large cotyledons and a highly reduced primary axis without a recognizable division into radicle and plumule. During imbibition the seeds secrete mucilage. On germination, the expanding cotyledons break open the seed coat and emerge out of it. The radicle fails to develop a root. Instead it forms several unicellular rhizoids which secrete gum. In *Griffithella* the gum has been shown to be a polysaccharide (Vidyashankari, 1988a). The cotyledons continue to elongate and reflex. A plumule is organized post-germinally and the first leaf-like structure appears one week after germination. The number of leaf-like structures formed by the plumule varies from species to species (unpublished work) after which the plumular activity ceases. Further development occurs by the transfer of meristematic activity to the hypocotyledonary portion. A small protuberance is formed, which develops into a dorsiventral, branched chlorophyllous thallus, typical of the respective species. In *Polypleurum stylosum*, thallus has also been observed to arise in a few instances from the cotyledons and leaf-like structures in the seedling. After expansion the thallus also bears leaf-like structures (Vidyashankari, 1988a)/secondary shoots (Willis, 1902) along the margins and rhizoids on the ventral surface. The ontogeny of these has not

been worked out in detail. The morphological nature of the thallus is also a matter of dispute. Nagendran (1975) believes that it represents a stem whereas Tulasne (1852), Warming (1891), Willis (1902) and Engler (1930) argue for its root origin. The work done by Vidyashankari and Mohan Ram (1987) on *Griffithella hookeriana* and by us on *Polypleurum stylosum* suggests that the thallus originates as an extension of the hypocotyledonary region of a young seedling.

Flower buds are initiated when the plants are submerged and the water level is 25-40 cm above the thalli. With the falling of the water level in the river, the thalli become exposed to the aerial environment. The leaf-like structures/secondary shoots gradually are replaced by reproductive shoots in the subsequent growth of the exposed thalli. There are no studies on the mechanism of pollination. Fruit development occurs above water. What factors initiate flowering in nature is not understood. Nevertheless, we have been able to induce flowering under *in vitro* conditions by subjecting the plants of *Polypleurum stylosum* and *Indotristicha ramosissima* to stress. The signals responsible for induction need further investigation.

**Table 1—Relationships between Podostemoideae and Tristichoideae***

| CHARACTERS | TRISTICHOIDEAE | PODOSTEMOIDEAE |
|---|---|---|
| **Dissimilarities** | | |
| Flowers | Trimerous | Dimerous |
| Perianth | Present | Absent |
| Spathe | Absent | Present |
| Stamens | 1-25 | Many (1 or 2 in Indian taxa) |
| Staminodes | Absent | Present |
| Pollen | Monads | Dyads |
| Ovary | Tricarpellary | Bicarpellary |
| Ovules | Many, bitegmic | Few to many, bitegmic |
| Pseudo-embryo sac | Organized after fertilization | Arises before fertilization |
| Embryo | Plumule differentiated (?) | Plumule not differentiated |
| **Similarities** | | |
| Embryo sac | Apinagia type Podostemum type | Apinagia, Podostemum and Polypleurum type |
| Fertilization | Single (only syngamy) | Single (only syngamy) |
| Endosperm | Absent | Absent |
| Embryogeny | Solanad type | Solanad type |
| Embryonal haustorium | Present | Present |

*Reproduced from Nagendran (1975).

## EMBRYOLOGICAL FEATURES

The Podostemaceae are recognized as an embryological family because of the several remarkable features not known in such combination in any other angiosperm family. Among the notable characteristics are lack of antipodals, absence of double fertilization and endosperm, presence of a pseudo-embryo sac and single fertilization (Razi, 1949; Maheshwari, 1955; Mukkada, 1962, 1969; Chopra & Mukkada, 1966; Kapil, 1970; Battaglia, 1971; Mukkada & Chopra, 1973; Nagendran, 1975; Nagendran & Arekal, 1976; Arekal & Nagendran, 1974, 1975a, b, 1977a, b; Nagendran *et al.*, 1981). Though syngamy is normal, the fate of the second male gamete is disputed (Mukkada, 1962; Walia, 1965; Chopra & Mukkada, 1966).

The family Podostemaceae has been divided into two subfamilies—Tristichoideae and Podostemoideae. Table 1 presents similarities and dissimilarities between the Podostemoideae and Tristichoideae regarding floral and embryological features (Nagendran, 1975). It is apparent that there are two distinct lines of evolution within the family.

## ORIGIN AND EVOLUTION

The origin and evolution of the Podostemaceae are perplexing questions. Willis (1915) believed that the ancestors of Podostemaceae must have been land plants. He presumed that they might have taken to water at one time and undergone whole of the evolution in water. It was a riddle for Willis to account for the origin of diverse morphological forms within the family under what he considered most uniform conditions provided by running water. He explained it as cumulative mutations without natural selection. He believed that the thallus had no adaptive significance to the plant and that Podostemaceae may have a continuum of genotypes with more specialized to less specialized forms. Tristichoideae are believed to be represented by three genera, whereas Podostemoideae include the others. Members of the family Tristichoideae are simple, less-specialized and more widespread (Willis, 1902). They have greater tolerance to environmental fluctuations and therefore occupy more trophic niches. The structure of *Indotristicha ramosissima* has been described in detail by Rutishauser and Huber (unpublished)*. According to them, the plant has creeping roots with several rhizoids on the ventral surface. It bears (a) secondary and tertiary roots with a root cap, (b)

*This work has since appeared in *Plant Systematics and Evolution 1991*, **178** : 195-223.

holdfasts, and (c) floating shoots with flowers at the tips. Several ramuli are produced on the shoots. It is in the tribe Tristichoideae that one finds the transition from regular erect branches to prostrate, flat and dorsiventral thalli. The trend towards dorsiventrality continues in the tribe Podostemoideae and even permeates the most conservative organ, i.e., flower (with the loss of some stamens and obliquity of gynoecium and seed) (Willis, 1902). In contrast to Tristichoideae, Podostemoideae are highly specialized and consequently occupy narrow niches. The seemingly simple structure of Podostemaceae appears to be a case of reduction.

## AFFINITIES

To the best of our knowledge, two fossil records of Podostemaceae are available from the Tertiary Period in Europe. These are: (i) *Podostemonopsis tertiaria* (Weyland, 1937) from Siebengebirge on the river Rhine, and (ii) *Podostemonites corollatus* (Szafer, 1952) from West Carpathian mountains. The latter has unisexual flowers, 3 sepals united in the middle, 3 free petals, 6 free stamens. Female flowers are not known. Stomata are present.

As only fragmentary information is available on the fossil Podostemaceae, it is difficult to throw any light on the affinities of podostemads. When Aublet discovered *Mourera fluviatilis* in 1775, he placed it with the monocots. In 1815, Richard described *Podostemon ceratophyllum* and raised it to the rank of a family, viz., Podostemeae, although he still considered this group to have monocotyledonous affinities. Subsequently it was placed among the dicotyledons by Lindley (1847). Bentham and Hooker (1880) placed this family in Multiovulatae Aquaticae of Monochlamydeae. Rendle (1925), Takhtajan (1966) and Cronquist (1988) have grouped it under Rosales, Rosidae (Magnoliatae) and Rosidae (Magnoliopsida), respectively. The pioneering works of Gardner (1847), Tulasne (1849), Warming (1901) and Willis (1902) have contributed immensely to the understanding of the

**Table 2—Embryological relationship with related families***

| CHARACTER | PODOSTEMACEAE | HYDROSTACHYDACEAE | SAXIFRAGACEAE | CRASSULACEAE |
|---|---|---|---|---|
| Anther wall | 4 or 5 layered | — | 4 layered | 5 layered |
| Anther tapetum | Secretory | Secretory | Secretory or amoeboid | Secretory |
| Microsporogenesis | Simultaneous or successive | Simultaneous | Simultaneous | Simultaneous |
| Pollen grains | Monads or dyads, shed at 2-celled stage | Compound, permanent in tetrads | Monads or tetrads | Monads shed at 2-celled stage |
| Gynoecium | 2 or 3 carpellary, ovary syncarpous 2 or 3 locular | Bicarpellary, syncarpous ovary unilocular | 2-5 carpellary syncarpous, 2-5 locular | Apocarpous |
| Ovules | Many, tenuinucellate bitegmic, on axile placenta | Many, tenuinucellate unitegmic, anatropous on parietal placenta | Many, crassinucellate or tenuinucellate bitegmic/unitegmic on axile placenta | Numerous on marginal placenta, anatropous crassinucellate, bitegmic |
| Megaspore tetrad | No linear tetrad formed | Linear | Linear/bisporic | Linear/T-shaped/ isobilateral |
| Embryo sac development | Bisporic, Apinagia Podostemum/Polypleurum type, mature embryo sac 4 or 5 nucleate | Polygonum type | Polygonum type and Allium type | Polygonum type |
| Antipodal cells | Absent (2 in *Dicraea* ?) | Present | Present | Present |
| Pseudo-embryo sac | Present | Absent | Absent | Absent |
| Embryogeny | Solanad, suspensor haustoria present | Onagrad type-Capsella variation, suspensor haustorium absent | Caryophyllad type, Sedum variation | Caryophyllad type, suspensor haustorium absent |

*Modified after Nagendran (1975).

Indian Podostemads.

Taxonomists have held various views concerning the relationships of the Podostemaceae with other angiosperm families. For example, Podostemaceae have been related to Saxifragaceae (Warming, 1888; Engler, 1930); Crassulaceae (Hutchinson, 1959); Hydrostachydaceae (Subramanyam, 1962). The embryological features of families related to Podostemaceae are presented in Table 2.

On the basis of embryological studies Maheshwari (1945) had observed that the Podostemaceae are much reduced apetalous derivatives of the Crassulaceae.

Thorough study is needed to understand and interpret the wide range of morphological and physiological variability of the family. Because of their endemic nature and habitat specialization, the podostemads are vulnerable to anthropogenic changes in the environment. There is justifiable need to conserve their biodiversity. Methods for their *in vitro* cultivation have been developed by our group, which makes their *ex situ* conservation and study a possibility.

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