

## = Marsileaceae =

The Marsileaceae / m??rs?li?e?si? / are a small family of heterosporous aquatic and semi @-@ aquatic ferns , though at first sight they do not physically resemble other ferns . The group is commonly known as the " pepperwort family " or as the " water @-@ clover family " because the leaves of the genus Marsilea superficially resemble the leaves of a four @-@ leaf clover ( a flowering plant ) . Leaves of this fern have sometimes been used to substitute for clover leaves on Saint Patrick 's Day . In all , the family contains 3 genera and 50 to 80 species with most of those belonging to Marsilea .

## = = Natural history = =

Members of the Marsileaceae are aquatic or semi @-@ aquatic . Plants often grow in dense clumps in mud along the shores of ponds or streams , or they may grow submerged in shallow water with some of the leaves extending to float on the water surface . They grow in seasonally wet habitats , but survive the winter or dry season by losing their leaves and producing hard , desiccation @-@ resistant reproductive structures .

There are only three living genera in the family Marsileaceae . The majority of species ( about 45 to 70 ) belong to the genus Marsilea , which grows worldwide in warm @-@ temperate and tropical regions . Marsilea can be distinguished from the other two genera by the presence of four leaflets on each leaf , although some species occasionally produce six leaflets per leaf . A second genus Regnellidium includes a single living species that grows only in southern Brazil and neighboring parts of Argentina ; it has only two leaflets per leaf . The third genus Pilularia grows widely in temperate regions of both the northern and southern hemispheres . Its leaves do not subdivide into leaflets but are slender and tapered to a point , so that it is often overlooked and mistaken for a grass . There are only about five species known .

The closest relatives of the Marsileaceae are the Salviniaceae , which are also aquatic and heterosporous . However , both of these other fern families float freely on the surface of ponds or lakes instead of rooting in soil or mud . The close relationship of these groups to the Marsileaceae is supported by both morphologic and molecular analysis , as well as by the discovery of an intermediate fossil named Hydropteris . In general , the Salviniaceae and Azollaceae have a much better fossil record than the Marsileaceae . Until recently , Rodeites dakshinii was the oldest fossil member known ; it is a preserved sporocarp containing spores , found in Tertiary chert of India . In 2000 , the discovery of fossilized sporocarps from the Cretaceous of eastern North America was announced . These fossils were assigned to the species Regnellidium upatoiensis , and pushed the known history of the Marsileaceae back into the Mesozoic . The oldest fossil known for the Marsileaceae is Regnellites nagashimae from the Upper Jurassic or Lower Cretaceous of Japan . The fossils include leaves with visible veins , as well as sporocarps .

## = = Morphology = =

The Marsileaceae share many of the basic structural characteristics common to most ferns , but the differences are more noticeable than the similarities . Species of this family have long , slender rhizomes that creep along or beneath the ground . Their fronds ( leaves ) grow in distinct clusters at nodes along the rhizome , with wide spacing between leaf clusters . As a result , the plants appear to be more stem than leaf , unlike other ferns .

Roots grow primarily from the same nodes as the leaves , but may also grow from other locations along the rhizome . The roots of Marsilea and Regnellidium are noteworthy for containing vessel elements . Vessels have also been found in the rhizome of two species of Marsilea . These vessels have evolved independently of vessels in other groups of plants .

The leaves are the most easily observed characteristic for the Marsileaceae ; they have a long slender leaf stalk ending in zero , two , or four ( occasionally six ) leaflets . The number of leaflets differs among the three genera and can therefore be used for identification . In Pilularia , the leaves

are narrowly cylindrical and taper to a point . Leaves of *Regnellidium* bear two broad leaflets , while leaves of *Marsilea* bear four leaflets at the tip . The four leaflets on the leaf of *Marsilea* are not borne equally . Instead , they are borne in pairs with one pair of leaflets attached slightly higher than the other . Thus in the developing leaf , the leaflets are folded more like the wings of a butterfly than like the leaflets of a clover .

As with other ferns , the leaves develop in a circinate pattern . They begin as small , tight spirals which unroll as the leaf matures . At full maturity they are held erect with the leaflets unfolded , except in *Pilularia* whose leaves have no blade . Temperate species are deciduous , losing their vegetative leaves in winter . Tropical species may also lose their leaves during the dry season . These leaves are photosynthetic , and produce most of the food used by the plant .

Some aquatic species of *Marsilea* , especially those growing with their rhizome submerged , may have vegetative leaves that are dimorphic . Some of their leaves grow up to the surface of the water , and look just like leaves of species growing out of water . These plants also produce other leaves with shorter leaf stalks that are not long enough to reach the surface , and so the leaflets remain underwater . These leaves have different anatomical and cellular characteristics better suited to their submerged environment .

In addition to their vegetative ( sterile ) leaflets , all species of *Marsileaceae* produce fertile ( spore @-@ producing ) leaflets at or near the base of the photosynthetic leaves . This reproductive portion looks and functions very differently from the vegetative portion of the leaves .

= = Life cycle = =

Like other ferns , members of the *Marsileaceae* produce spores , but not seeds when they reproduce . Unlike other ferns , the spores in this family are produced inside sporocarps . These are hairy , short @-@ stalked , bean @-@ shaped structures usually 3 to 8 mm in diameter with a hardened outer covering . This outer covering is tough and resistant to drying out , allowing the spores inside to survive unfavorable conditions such as winter frost or summer desiccation . Despite this toughness , the sporocarps will open readily in water if conditions are favorable , and specimens have been successfully germinated after being stored for more than 130 years . Each growing season , only one sporocarp typically develops per node along the rhizome near the base of the other leaf @-@ stalks , though in some species of *Marsilea* there may be two or occasionally as many as twenty . The resemblance of the sporocarps to peppercorns gives the family its common name of pepperwort .

The sporocarps are functionally and developmentally modified leaflets , although they have much shorter stalks than the vegetative leaflets . Inside the sporocarp , the modified leaflets bear several sori , each of which consists of several sporangia covered by a thin hood of tissue ( the indusium ) . Each sorus includes a mix of two types of sporangium , each type producing only one of two kinds of spores . Toward the center of each sorus and developing first are the megasporangia , each of which will produce a single large female megaspore . Surrounding them at the edge of the sorus and developing later are the microsporangia , each of which will produce many small male microspores .

Because the *Marsileaceae* produce two kinds of spore ( and thus two kinds of gametophyte ) , they are called heterosporous . While heterospory is the norm among all plants with seeds , such as the flowering plants and conifers , it is very rare among other groups of plants . Also , most heterosporous plants produce their two kinds of sporangia in different places on the plant . Since the *Marsileaceae* grow both kinds together in a single cluster , they differ from other plants in this regard as well .

The spores remain dormant inside the sporocarp through unfavorable conditions , but when conditions are suitable and wet , the sporocarp will germinate . It splits into halves , allowing the tissue coiled inside to become hydrated . As this internal tissue swells with water , it pushes the halves of the hard outer covering apart , and emerges as a long gelatinous worm @-@ like sorophore . The sorophore is a sorus @-@ bearing structure unique to the *Marsileaceae* ; it may extend to more than ten times the length of the sporocarp inside which it was coiled . This extension

carries the numerous spore @-@ producing sori attached along each side of the sorophore out into the water .

= = Human uses = =

Some species of Marsilea are cultivated in garden pools or aquaria . The Indigenous Australians once made a porridge of pulverized Marsilea sporocarps called nardoo . However , the sporocarps contain toxic levels of thiaminase , so careful preparation methods must be used in order for the nardoo to be safe for consumption .