

## **Higher spore plants**

### **Plan**

- 1. Higher plants. Peculiarities of air habitat.**
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- 3. The Bryophyta division.**
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Higher plants (Embryophyta, Embriobionta) - sub-kingdom of the Plantae kingdom; complex differentiated multicellular organisms, adapted to life in a terrestrial environment, with the correct alternation of sexual (gametophyte) and asexual (sporophyte) generations. Distinguish between spore and seed higher plants.

Higher plants include all leafy plants which reproduce by spores or seeds. Most of them are terrestrial. The origin of higher plants is related to the entry into the land.

Embryophytes are primarily adapted for life on land, although some are secondarily aquatic.

It is believed that the ancestors of higher plants were green water plants of fresh or brackish-water bodies of water.

The evolutionary origins of the embryophytes are discussed, but they are believed to have evolved from within a group of complex green algae during the Paleozoic era (which started around 540 million years ago) probably from terrestrial unicellular charophytes, similar to extant Klebsormidiophyceae.

On a microscopic level, the cells of embryophytes are broadly similar to those of green algae, but differ in that in cell division the daughter nuclei are separated by a phragmoplast. They are eukaryotic, with a cell wall composed of cellulose and plastids surrounded by two membranes. The latter include chloroplasts, which conduct photosynthesis and store food in the form of starch, and are characteristically pigmented with chlorophylls a and b, generally giving them a bright green color. Embryophyte cells also generally have an enlarged central vacuole enclosed by a vacuolar membrane or tonoplast, which maintains cell turgor and keeps the plant rigid.

### **Peculiarities of air (terrestrial) habitat**

- Parts of a plant are in two different environments (air and soil), which led to differentiation into two systems of organs - underground and above-ground with fundamentally different functions.
- In the air environment, unlike in the water environment, protection from moisture loss and appropriate adaptations are necessary.

- Transpiration, the most important mechanism of metabolism (water and gases), becomes possible and necessary in air environment; it allows the transfer of substances within a plant (upward flow).
- Gravity is not compensated by Archimedes' force and the development of mechanical tissues becomes necessary.
- The sexual process still requires water, and it requires the development of various adaptations, which further led to the formation of the flower.

When plants became land-dependent, they developed various adaptations to new habitats providing water, protection against drying out and support of sexual reproduction. There appeared tissue systems: covering, conducting, mechanical. They have organs performing various functions: the root (rhizoids), stem and leaf. Significant changes occurred in the structure of sexual and asexual reproduction. There appeared multicellular receptacles of spores - sporangia and multicellular sexual organs protected by layers of sterile cells.

**The life cycle** of higher plants consists of two rhythmically alternating phases (or generations) - the sporophyte (asexual) and gametophyte (sexual). The sexual organs develop on the gametophyte. Gametophyte can be monosexual (male or female) or double-sexed. Sexual organs develop on the gametophyte: female organs - archegonia and male organs - anteridia. Sex cells - gametes (male or female) are formed in the sexual organs. Fertilization occurs within the female reproductive organs - archegonium. As a result of fertilization a zygote with a diploid set of chromosomes is formed. Sexual process is oogamous (large immobile ovule, which does not drop the sex organ and a small mobile sperm). In higher plants, unlike in lower plants, a multicellular embryo is formed from the zygote. As a result of growth and development, a sporophyte is formed from the embryo. All cells of the sporophyte have a diploid set of chromosomes. The sporophyte forms the organs of asexual reproduction - sporangia - in which spores develop by reductive division (meiosis). Spores are haploid and give start gametophyte. Thus, the change of sexual and asexual generation in higher plants occurs during spore formation and fertilization (zygote formation). In some higher plants (psyllots, plau-nas, horsetails, ferns), the sporophyte and gametophyte are independent organisms; in others, one of two generations is subordinated to the other and is physiologically reduced to its organ

The subkingdom of higher plants includes the following Divisios:

**Rhinophytes – Rhyniopyta**

**Bryophytes - Bryophyta**

**Lycopods - Lycopodiophyta**

**Horsetails - Equisetophyta**

**Ferns - Polypodiophyta**

**Gymnosperms - Pinophyta**

**Angiosperms (flowering) - Magnoliophyta.**

**The Rhyniophytes** are a group of extinct spore-bearing vascular plants that were leafless and rootless plants, with upright branching stems. This group is the earliest known representatives of the higher plants, possessing true vascular tissue. This group gets its name from the locality from which they are found in Rhynie Scotland. The Rhynie Chert shows exquisitely preserved fossils, providing evidence of the entire life cycle of Rhynia. These plants had ground-creeping rhizomes, that gave rise to upright determinate stems. Unlike most plants of the Devonian, they had adventitious branching with latent "buds" or branches. In addition, this locality provides evidence of the gametophyte phase.

#### *Features*

*Sporophyte (spore-bearing phase)*

*Aerial stems: above ground, upright stems which terminate in sporangia for dispersal*

*Branching is isotomous, anisotomous, and even pseudomonopodial*

*Rhizomes: ground-running, or below ground portions, that creep similar to vegetative propagate the population*

*Mycorrhizae are found in the cortex of Rhynia rhizomes*

*Adventitious branching: latent "buds" or branches, which could elongate to make new stems, similar to modern plants.*

*Vascular tissue present, but consist only tracheids, without vessels.*

*Leafless; assumed by some to have photosynthetic stems and/or rhizome.*

*Gametophyte may have been the main photosynthetic portion of lifecycle*

*Spores in sporangia*

*Gametophytes dioicous\*, bearing male and female gametangia (antheridia and archegonia) on different axes*

*\*Note that in gametophytes, the term is "dioicous", not "dioecious" as in sporophytes*

*Gametophyte axes are vascular, unlike all gametophytes of modern pteridophytes (except for Psilotum)*

## **Divisio Bryophytes - Bryophyta**

Very often they referred to by the popular and short name mosses, which refers to only one class of this division, the leaf-forming mosses.

About 10,000 species of small plants, found almost everywhere except in highly saline deserts, belong to this division. Among higher plants, the mosses occupy a separate position. This is a very ancient group that existed in the Carboniferous period. The science studying moss-like plants is called bryology.

Mosses are a separate branch of evolution of higher plants, which took the way of the highest development of gametophyte and its prevalence over sporophyte. Their sizes are small, the largest up to 60 cm in height. However they play the important role in vegetation cover of the Earth, often forming continuous coverage of tundras, taiga (boreal) forests, raised bogs and swamps, high-moor forests, etc. In arid areas (in particular, in our region) there are also often habitats where

mosses play not the last role. Most mosses are perennial plants, forming relatively dense tussocks. The body structure of mosses is very primitive. Their gametophytes often (in the class of leafy mosses and liverworts) form organs similar to stems and leaves of sporophytes of other higher plants. In bryology, the terms caulidia and phyllidia are used for them, respectively.

The peculiarity of the development of these organisms is the predominance of the haploid stage, the gametophyte, in the life cycle. The spore of mosses produces a protonema. It may be filamentous or lamellate. Numerous buds are established on it, from which, in their turn, gametophyte plants grow. Therefore, mosses often form clumps. Moss gametophytes are usually either male or female, but both grow from the same protonema. The sexual organs, anteridia and archaegonia, are formed on the gametophytes. Fertilization occurs in the archegonia, where the sperm enters with droplet-liquid moisture (drops of rain, dew, etc.). A sporophyte develops from the zygote formed as a result of fertilization. The sporophyte of mosses is extremely reduced and consists of a capsule, a seta and a suction cup - gaustoria. It feeds on the gametophyte and is called a sporogon. The structure of the boll differs in different groups of mosses. Inside it is a spore sac, in which, by means of reduction division (meiosis), spores are formed.

The Mosses are divided into three classes: **Anthocerotopsida, Marchantiopsida or Hepaticopsida, and Bryopsida.**

Marchantiopsida or Hepaticopsida, the representative is *Marchantia polymorpha*. The gametophyte is in the form of a lamellate thallus, 10-12 cm long, branching apically. On both sides it is covered by epidermis. Upper epidermis has ventilation holes - stomata. They are surrounded by special cells arranged in four rows. Under the stomas, there are air chambers. The lower epidermis produces outgrowths - unicellular rhizoids and reddish or greenish scales, which are sometimes mistaken for reduced leaves. Under the upper epidermis is assimilatory tissue, consisting of vertical columns of parenchyma cells with chloroplasts. Below is a layer of thin-walled chlorophyll-free parenchyma cells. On the upper side of the thallus, special twigs - stands are formed, and on them are the organs of sexual reproduction. *Marchantia* is a dioicous plant. On some specimens, gametangiophores in the form of a nine-rayed star, with archegonia located between the rays on the underside. On others, the gametangiophores take the form of an octagonal shield sitting on the seta, on the upper side of which are antheridia immersed in antheridial cavities. An egg cell is formed in the abdomen of the archegonium. After its fusion with a sperm cell, a sporogon is formed from the zygote. It is a capsule on a short seta, which is attached to the gametophyte by gaustoria. Inside the capsule haploid spores and elaters are formed. The spores are formed from sporogenic cells as a result of meiosis. The elaters are dead elongated cells with spirally thickened walls, serving to loosen the mass of spores as well as to eject them from the boll.

Vegetative propagation is accomplished by green, lens-shaped brood bodies (gemma). They are formed on the upper side of the thallus in special baskets (gemma cups) as a result of the division of the cells lining their bottoms.

**True mosses (Bryopsida)** -The gametophyte is an erect stem-like axis covered with leaf-like outgrowths. Conventionally, they can be called stem and leaves. On the lower part of the stem, multicellular rhizoids are formed. Branching is lateral. Axial growth occurs as a result of division of the pyramidal apical cell. It can be monopodial or sympodial. Accordingly, the organs of sexual reproduction and sporogonium are placed on the apex of gametophyte or on the lateral ramifications.

The class is subdivided into three subclasses: Andree mosses, Sphagnum mosses Subclassis *Sphagnidae*, and True (Green) mosses (Bryidae). The last two subclasses are the most important.

**Sphagnum mosses** have a rather uniform structure. Their gametophyte is a strongly branched plant, especially in the upper part. The ramifications are densely covered with leaves. Sphagnum mosses live in a very humid environment. As a result, they have no rhizoids, and moisture flows directly into the stem, which dies off at the base over time. The leaf consists of a single row of cells, differing sharply both in structure and in the function they perform. Some of them are living, chlorophyll-bearing, others are dead, relatively larger, with spirally thickened walls, pierced with holes; they are called hyaline cells. Hyaline cells can accumulate and retain a huge amount of water, 30-40 times more than the weight of the plant itself. The sporogon consists of a stalk (seta) and a capsule. The seta is strongly shortened, bulb-like, but by the time the spores become mature, the gametophyte stem tip grows strongly, extending the capsule upward (false seta). In the center of the capsule there is a rounded column, above which a sporangium with sporogenic tissue is arranged in the form of an arch. The wall of the capsule is strong, multi-layered. The capsule has a lid, which bounces off during the maturation of the spores, and the spores disperse. There is no elateres.

The importance of sphagnum in nature is very great. By accumulating huge amounts of water and growing by dense turf, they cause the swamping of vast areas, reaching to the tundra zone. Agromeliorative works are carried out to dry them. On the other hand, old bogs are of great economic importance for the development of peat deposits. The growth of the peat layer in the most favorable conditions is slow - a layer of 1 cm thickness is formed in about 10 years.

**True (green) mosses** - Compared to sphagnum mosses, brie mosses have a more diverse structure. The organs of sexual reproduction in some species are laid down on the main axis, in others on lateral axes. Branching is not manifested in some species.

*Polytrichum commune* cuckoo flax, is one of the common representatives of brie mosses. It grows in forests, glades, and the outskirts of bogs. The stem of the gametophyte is erect, nonbranched, 15 cm or more in height, densely covered with leaves. Its underground part spreads almost horizontally in the soil, where rhizoids are formed. Leaves are arranged in a spiral pattern. They consist of a linear lamina with a pointed toothed apex and a filmy sheath. Gametophyte is dioicous. Capsule upright or more or less obliquely arranged, prismatic, four- to five-sided, covered with a fibrous calyptra formed from the walls of the archaegonium. Capsule con-

sists of capsule and operculum. The lower part of the capsule is narrowed into apophysis. In the center of the capsule is a columella. Around the columella is a sporangium in the form of a cylindrical sac, attached to the wall and columella by special filamentous formations. The capsule has a special device for dispersal of spores, the peristome, which is a series of teeth with blunt apices located along the edge of the capsule. There are holes between the teeth, through which spores are dispersed in dry weather. Protonema in the form of green branching filaments grows from the spore. Buds are formed on it, from which adult gametophytes eventually develop.

### **Divisio of Lycopodiophyta.**

Lycopods are among the most ancient of the higher plants. They represent a fine-leaved evolutionary lineage. Modern species are perennial evergreen, herbaceous plants; among the extinct ones, there were woody forms as well. Many species are now extinct. Among the lycopodiophyta (Lycopodiophyta) there are equal-lysporous and heterosporous plants. Plants of different spores have leaves with tongues. Spores of lycopods usually have a three-beam scar. Gametophytes of dissipated lymphoids are unisexual, non-green, usually develop within several weeks due to the nutrients contained in the spore, and upon reaching maturity do not protrude outside the spore envelope.

The division is divided into two classes: the Lycopodiopsida and the Isoëtopsida.

**The class of Isoetopsida** includes heterosporous lycopods. This includes the orders: Selaginellales, Lepidodendrales and Isoetales, with Lepidodendrales completely extinct, and the other two orders are represented by living plants. It is with a tongue, and with adventitious roots, usually extending from a thin stem; some fossils had a well-developed rhizophore. Sporangia are located on the stem near the leaf axil or in the leaf axil. Sporophylls are collected in strobiles. Gametophytes are unisexual, small, develop throughout the year without leaving the spore membrane, due to the reserves of nutrients in the spore. Spermatozoa are biflagellated.

Modern representatives are a member of the genus *Selaginella*. The main way of reproduction of *Selaginella* is asexual reproduction using spores. The strobili are located at the ends of the side branches. They are either quite sharply demarcated from the rest of the leafy shoot, or outwardly almost indistinguishable from it. Sporophylls sit on the axis of the strobil in a spiral or oppositely opposite in 4 longitudinal rows. Perennial, herbaceous evergreens with simple, narrow leaves. Spores of haploid isospores develop in sporangia collected in strobiluses.

### **The class Lycopodiopsida**

Sporophytes are herbaceous perennial plants. The sporophyte has an above-ground shoot with small, sometimes scale-like leaves. They are poorly differentiated, with 1-2 nonbranched veins. Nodes and internodes are weakly expressed. The underground part of the sporophyte is represented by a rhizome with adventitious roots. Branching of above- and below-ground axes is apical. Sporangia are located

on the upper side of leaves (sporophylls), aggregated on the ends of axes in spikelets. The stem and root have no cambium. Leaves have no ligulas. Spores are of equal size. Gametophytes are double-sex, underground, saprotrophically feeding, and mature within 1-15 years. Two genera are represented in the modern flora. The most numerous and widespread of them is the genus *Lycopodium*. Economic importance of *Lycopodium*s is small. Animals do not eat them. They are used as a raw material for the production of medicines. Since ancient times they use *Lycopodium* spores that contain non-drying oil. They are used as baby powder, and sometimes in shaped molding for sprinkling the walls of models, so that the cast part had smooth walls and was easy to separate from the mold.

***Lycopodium clavatum*.** A plant widely distributed in coniferous forests. The sporophyte is represented by a long creeping shoot with vertical offshoots and adventitious roots. One vascular bundle is located in the center of the stem. The central cylinder occupies a small part. A broad area of the cortex is pierced with leaf traces. The leaf blade is linear, smooth-edged, ending in a long, thin hair.

Spore-bearing strobiluses crowning vertical shoots, are arranged on fairly long stems two by two (less often 3-5). Strobiluses are cylindrical, consisting of an axis, on which densely sporophylls, triangular-shaped scales with tips pointed and curved upward, sit. On the upper side of the sporophyll is a bud-shaped sporangium with spores on a short stalk. Spores are identical, small, tetrahedral in shape.

The sporangium is dehiscence by a transverse slit. Spores fall to the ground, and, at a depth of a few centimeters a gametophyte slowly develops from them, over a period of 12-15 years. It takes the form of a bulb, growing later to saucer-shaped, up to 2 cm in diameter. Gametophyte is colorless. Cells under epidermis are in symbiosis with mycelium of fungus. In some species, the gametophyte is formed on the soil surface, and then chloroplasts appear in its cells. Antheridia and archaegonia are placed on the upper side and are immersed in the parenchyma. The spermatozoa are numerous, biflagellate. Fertilization is connected with water. A zygote does not have a dormant period; a sporophyte embryo is formed from it immediately. It is initially integrated in the gametophyte tissue and feeds to some extent on it, but soon its roots penetrate into the soil, and the sporophyte begins its long independent life.

### **Divisio Equisetophyta.**

The overwhelming majority of Equisetophyta are homosporous plants, and only a few fossil forms were heterosporous. Perennial, low stiff grasses with whorled side shoots and small whorled scaly leaves, the stems are impregnated with silica.

Spores are haploid, heterospores, formed in spore-bearing spikelets consisting of scutes on spring shoots. Representatives: Field horsetail, meadow

Arboreal representatives are completely extinct; only herbaceous ones have survived in the modern flora.

A characteristic feature of the sporophyte is lateral branching with whorls of lateral shoots. Leaves are also assembled in whorls. Nodes and internodes are clearly expressed. At the base of internodes, there is often an intercalary meristem.

Leaves are reduced, medium to small, with one central vein. Chloroplasts do not contain pyrenoids. Sporangia are located on sporangiophores, which are homologues of sporophylls but differ in structure from them. Modern Equisetaceae is equisporeal. Spores of the same size form differently sexed gametophytes (female, male or double sex). There are special outgrowths on the outer membrane of spores - elateres. Elateres have a dual function: spreading spores and joining spores into groups, which ensures joint growth of male and female gametophytes.

Gametophytes are small, a few millimeters in size, green, female, male or double sex. Fertilization is related to water. Embryo has no dormancy period.

The division is subdivided into four classes: Hyenopsida, Sphenophyllopsida and Equisetopsida. The first two classes and Calamites (Equisetopsida) are extinct. The horsetails are present in the modern flora of both hemispheres.

We will consider the horsetails.

The class includes one genus, the horsetail (*Equisetum*). Total number of species is 30-35, in our country - 13. Widespread throughout the globe, except Australia. They grow mainly in damp habitats. Overground shoots of horsetails, as a rule, are annual, only in a few species - perennial, evergreen. Most species have epidermal cell walls encrusted with silica. Many species are difficult to eradicate weeds of pastures and fields, especially those with acidic soils (field horsetail - *E. arvense*). Some species are poisonous to domestic animals (swamp horsetail - *E. palustre*, oak horsetail - *E. nemorosum*). Horsetails are used as medicinal plants. Their stems are used instead of sandpaper.

Field horsetail (*Equisetum arvense*) is one of the most widely distributed species. This is a perennial herbaceous plant. It grows in fields and fallows as a weed. Its underground part is represented by a rhizome penetrating into the soil to a depth of 1 m. Some shortened lateral rhizome branches turn into tubers, which are filled with reserve starch. Leaf sheaths and adventitious roots are arranged in whorls at the nodes. The root has a primary structure, with large air-bearing cavities in the cortex. There are two types of aboveground shoots: spore-bearing, appearing in early spring, and sterile, appearing later and vegetating until late fall. Other horsetail species have the same above-ground shoots. Sterile shoots are whorled, branched, green, ribbed, at the nodes bear sheaths of leaves fused into tubes and ending with black teeth with white border. The denticles are reduced leaf blades. Since the leaves are reduced, the stem serves as the photosynthetic organ.

Sporiferous shoots are thicker, brown, without chlorophyll, nonbranched, 15-30 cm high. They are also covered at the nodes by tubular sheaths with 8-9 large teeth. Sporiferous strobiluses are formed at the apex. After sporulation, these shoots die off. Sporangiphore consists of hexagonal scutellum, a stalk, which attaches scutellum to strobilus axis, and sacciform sporangia along lower edge of scutellum. The spores are of equal size. Elateres look like spirally twisted ribbons with spoon-shaped extensions at the ends. Chlorophyll-bearing gametophytes grow from spores on the soil in the form of lobate plates, which are physiologically distinct. Some are male, with antheridia forming multiflagellate spermatozoa; others are female, with archegonia. Fertilization is associated with water. The sporophyte



embryo has no dormant period. Thus, the morphological homosporous of this species is combined with physiological heterosporous.

### **Divisio Fern (Polypodiophyta)**

The Polypodiophyta emerged at about the same time as the horsetails. At present there are more than 10 thousand species of ferns. Ferns are distributed all over the globe in various habitats, from tropical forests and swamps to deserts. Their species are most diverse in humid forests where they grow not only on the soil but also on other plants as epiphytes.

The sporophytes of ancient ferns were woody plants with column-shaped nonbranched trunks having radial symmetry. Modern fern-like plants are in most cases perennial herbaceous plants.

Unlike other higher spore plants, fern-like plants represent a large-leaved lineage of evolution. The leaves grow by top for a long time, they are called fronds. In most cases, leaves combine two functions: photosynthesis and spore production. In some species, the upper leaves specialize in spore production and the lower leaves in photosynthesis. Most species are homosporous but there are also heterosporous species.

The typical fern, a sporophyte, consists of stem, leaf, and root; it produces spores; and its cells each have two sets of chromosomes. The sporophyte of most ferns is perennial (it lives for several years) and reproduces vegetatively by branching of the rootlike underground stem, or rhizome, often forming large, genetically uniform colonies, or clones. A few ferns propagate by root proliferations, and some, especially in the wet tropics, reproduce by leaf proliferations. The spores are haploid; that is, they have one set of chromosomes. They are produced in specialized organs—the spore cases, or sporangia—on the fern leaves (fronds). Once released, the spores are carried by wind currents, and a small percentage of them fall in appropriate germination sites to form the sexual plants, or gametophytes. In ferns the gametophytes are commonly referred to as prothallia, and they are best known to biologists as laboratory objects in artificial culture. They are rarely observed in nature without arduous searching, and the gametophyte stage of the majority of fern species has never been seen in the wild.

The prothallia are tiny—usually less than 8 mm (0.3 inch) long—and kidney-shaped in the majority of species. They grow only until the new sporophyte has been formed by fertilization; then they wither and die in most species. The process of fertilization is accomplished by sperm and eggs produced upon the same or more commonly different gametophytes, and both the fertilized egg (zygote) and the resultant embryo are held within the tissues of the prothallium until the embryo grows out as an independent plant. Exceptions to this life cycle include several aquatic genera with separate megaspores and microspores, in which the gametophytic phase is reduced and remains largely within the spore walls. Also, many ferns are apomictic; that is, they produce spores with the same number of chromosomes as found in the sporophyte, and new sporophytes arise directly from cells of the gametophyte without the need for gametes or fertilization.

Polypodiophyta are an important component of many plant communities, especially of tropical, subtropical and northern broad-leaved forests. They are objects of decorative floriculture in indoors and outdoors, as well as raw materials for medicines.

*Dryopteris filix-mass*) is widely distributed in deciduous forests in damp shady places. Sporophyte is a perennial herbaceous plant up to 1 m tall. The shoot is represented by an underground rhizome. It is short, thick, black-brown in color, with a well-pronounced dorsoventral structure (the upper surface bears leaf petioles, the lower surface bears fine adventitious roots) and terminates in an apical bud consisting of a cone of growth surrounded by young leaves.

The semi-evergreen leaves have an upright habit and reach a maximum length of 150 cm (59 in), with a single crown on each rootstock. The leaf blade is elliptically oblong in shape, bilaterally Segments of the first order are arranged alternately, acuminate; segments of the second order (pinules) have a serrated margin and blunt apex. The bipinnate leaves consist of 20–35 pinnae on each side of the rachis. The leaves taper at both ends, with the basal pinnae about half the length of the middle pinnae. The pinules are rather blunt and equally lobed all around. The stalks are covered with orange-brown scales. On the lower (abaxial) side of the leaf, along middle veins of second-order segments, there are groups of sporangia, or sori, covered with a kidney-shaped membranous scales (indusium), attached to the leaf outgrowth, the placenta. On the abaxial surface of the mature blade 5 to 6 sori develop in two rows. When the spores ripen in August to November, the indusium starts to shrivel, leading to the release of the spores.

Sporangium is lenticular in shape with a long stalk and is also attached to the placenta. The shell of the sporangium is multicellular, single-layered. Among the thin-walled cells, there is a row of cells with horseshoe-shaped thickened walls that surrounds the sporangium in a narrow band. The ring of these cells is not closed. When the sporangium dries out, the ring cells are compressed and the shell in the thin part is ruptured and the spores are released. The spores are of the same size, oval in shape, and tuberculate. Meiosis occurs during spore formation.

A gametophyte (prothallia) grows from a spore in favorable conditions. It looks like a green round-core plate, up to 4 mm in diameter, attached to the soil by rhizoids. On the underside, near the notch, there are archaegonians with abdomen submerged in gametophyte tissue, and in the rhizoidal part there are rounded antheridia. Fertilization is connected with water. A sporophyte embryo grows from the zygote.

*Salvinia*, a genus in the family *Salviniaceae*, is a floating fern named in honor of Anton Maria Salvini, a 17th-century Italian scientist. Watermoss is a common name for *Salvinia*. Twelve species are recognized.

*Salvinia* is related to the other water ferns, including the mosquito fern *Azolla*. Recent sources include both *Azolla* and *Salvinia* in *Salviniaceae*, although each genus was formerly given its own family.

*Salvinia*, like the other ferns in order *Salviniales*, are heterosporous, producing spores of differing sizes. However, leaf development in *Salvinia* is unique.

The upper side of the floating leaf, which appears to face the stem axis, is morphologically abaxial.

Small, floating aquatics with creeping stems, branched, bearing hairs on the leaf surface papillae but no true roots. Leaves are in trimerous whorls, with two leaves green, sessile or short-petioled, flat, entire and floating, and one leaf finely dissected, petiolate, rootlike and pendent. Submerged leaves bearing sori that are surrounded by basifixed membranous indusia (sporocarps).

They bear sporocarps of two types, either megasporangia that are few in number (approximately 10), each with single megaspore, or many microsporangia, each with 64 microspores. Spores are of two kinds and sizes, both globose, trilete. Megagametophytes and microgametophytes protruding through sporangium wall; megagametophytes floating on water surface with archegonia directed downward; microgametophytes remaining fixed to sporangium wall.

The small, hairlike growths, known as trichomes or microgametical follicles, are not known to have any productive function, and are currently a biological mystery.

*Psilotum nudum*, one of two species in the genus *Psilotum*, is widely distributed across tropical and sub-tropical areas of the Americas, Africa, Asia and Australasia, with a small, endangered population found in southern Spain. *Psilotum* was long considered a 'fern ally', a surviving remnant of an extinct Devonian flora (because of its apparent similarities to the fossil plant *Rhynia*). However, recent molecular evidence places it within the true ferns and suggests a close relationship to the *Ophioglossaceae*, a family of ferns that includes the curious ferns called moonworts (*Botrychium*).

*Psilotum* is the only living vascular plant to lack both leaves and roots, hence the generic name that derives from the Greek word for bare or smooth. The dominate phase of the whisk fern life cycle, the sporophyte, has distinctive dichotomously branching stems which are solely responsible for photosynthesis and gas exchange. In place of leaves, the stems bear minute scales (enations) that lack vasculature. Prominent reproductive bodies, comprising three fused sporangia, are borne in the axils of enations on the upper parts of stems. Moisture is absorbed through hair-like rhizoids into a basal rhizome. The other stage of the whisk fern life cycle, the gametophyte, is completely subterranean and resembles a piece of rhizome. However, the gametophyte is unable to photosynthesize so is nourished by endomycorrhizal fungi; this unusual arrangement is also found in the *Ophioglossaceae*.

Whisk ferns are evergreen plants that grow in a variety of habitats, such as lithophytes in cracks in rock faces or epiphytically where humus accumulates in the forks of tree branches or wide leaf bases of palms. Whisk ferns generally have an erect habit, reaching a height of 50 cm. The other species in the genus, *Psilotum complanatum*, readily hybridises with *Psilotum nudum* to form the hybrid *Psilotum xintermedium*.

*Psilotum nudum* became a popular pot plant in Japan during the Edo period leading to the selection of many different cultivated varieties with evocative names

*such as 'Flying Cloud Pavilion'. Dozens of these varieties are illustrated in the Matsubaran fu, a list of cultivars published in 1836. Psilotum is difficult to grow from spores and is usually propagated by divisions. Despite that, it often appears spontaneously in glasshouse collections.*

*The plants have a variety of historical uses in Hawaii where spores were collected and used in the same way as talcum powder, while the stems, known as 'chickens' feet' were used in a children's game.*

As a group of plants, ferns are not of great economic value. Many different species have been used as a minor food source and for medicine in various parts of the world. Edible fern crosiers (young leaves with coiled hook-shaped tips) are popular in some areas. The ostrich fern (*Matteuccia*) of northeastern North America and of boreal parts Russia is frequently eaten, apparently with no ill effect, but the two ferns most commonly consumed in East Asia (*Osmunda* and *Pteridium*) have been shown to be strongly carcinogenic. The minute aquatic mosquito fern (*Azolla*) has become a valuable plant, especially in Southeast Asia; a blue-green algae (*Anabaena azollae*) is always found in pockets on the leaves of *Azolla* and helps convert nitrogen to a form usable by other plants (see nitrogen-fixation), thus greatly increasing the productivity of rice paddies where the fern occurs. The greatest economic value of ferns has been in horticulture, with large nurseries supplying millions of plants annually for both indoor decoration and outdoor gardens and landscaping. On the negative side, the poisonous bracken (*Pteridium aquilinum*), which often spoils the grazing value of various lands, is considered a noxious weed in many countries.

A major value of ferns is in biological research, for they have retained a primitive life cycle involving two separate and more or less independent generations, or growth phases, the plants of which are wholly different in many respects. Water ferns (genus *Ceratopteris*), which have relatively short life cycles and for which many mutations have been characterized, have become model organisms for genetics teaching and research.

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