1. Habit of Marsilea 2. Structure of Marsilea 3. Reproduction.

Habit of Marsilea:

The plants are herbaceous with rhizomatous stem, creeping on or just below the soil surface.

The species of Marsilea are generally aquatic or amphibious in nature with their roots embedded in mud or damp soil. The aquatic species — M. minuta and M. quadrifolia — occur in fresh water ponds, shallow water, or in mud or damp soil.

When grown in water, the whole body is submerged with just the leaf lamina floating on the surface of water. The amphibious species, M. aegyptiaca occur in seasonally wet habitats which produces reproductive structures during the drier periods.

M. condensata and M. rajasthanensis are near xerophytic forms which grow in dry soil. M. hirsuta is an extremely xerophytic plant reported from Australia.

Structure of Marsilea:

Sporophyte:

The sporophytic plant body of Marsilea shows differentiation of stem, leaves and roots (Fig. 7.116).

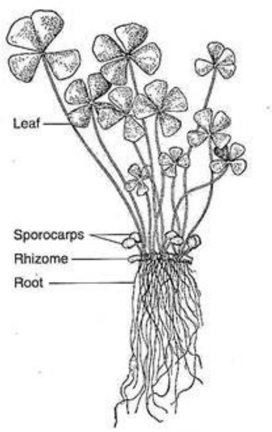

Fig. 7.116 : *Marsilea minuta*

1. Stem:

The stem is long, slender and freely-branched rhizome of indefinite growth that grows on or just below the soil surface. It is differentiated into nodes and internodes. The internodes are generally long in aquatic species but are short in sub- terrestrial or terrestrial species. The production of underground tubers on rhizome has been reported only in M. hirsuta.

A T.S. of the rhizome (stem) shows epidermis, cortex and the stele from periphery to the centre (Fig. 7.11 7).

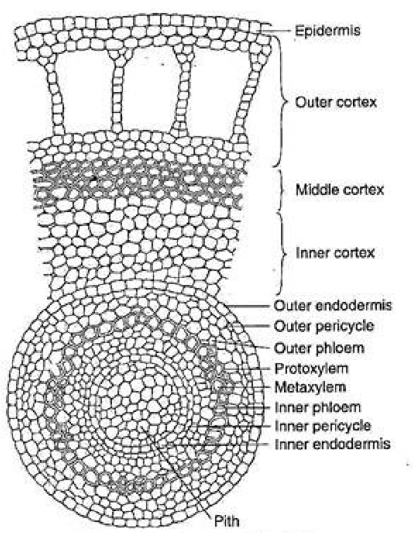

Fig. 7.117 : *Marsilea minuta*. T.S. of rhizome

The outermost layer is epidermis, composed of compactly arranged thick-walled cells and are devoid of stomata. The cortex is extensive and differentiated into three layers viz., outer cortex, middle cortex, and inner cortex. The outer cortex is parenchymatous with large air spaces.

The air chambers are separated from each other by a single-layered septum. The middle cortex is sclerenchymatous, while the inner cortex is made up of compactly arranged parenchymatous cells. The air spaces are absent in xerophytic species (e.g., M. aegyptiaca).

The stele is amphiphloic solenostelic which occupies the centre of the rhizome. Xylem occurs in the form of a ring and is surrounded on either side by phloem.

The central part of the stele is occupied by pith which is parenchymatous in aquatic species and sclerenchymatous in xerophytic species (e.g., M. aegyptiaca). The stele is bounded externally by outer pericycle and outer endodermis, while it is bounded internally by inner pericycle and inner endodermis.

2. Leaves:

The leaves arise from the nodes and are arranged alternately in two rows on the upper side of the creeping rhizome. The leaves are long petiolate and palmately compound, each having four leaflets in many species, but sometimes the number of leaflets varies from 3-8. A young leaf shows circinate vernation. At maturity the pinnae are extended perpendicular to the petiole. The venation is of closed reticulate type.

In T.S., the petiole differentiates into epidermis, cortex and stele (Fig. 7.118). The epidermis is cutinised and composed of a single-layered rectangular cells.

The cortex is differentiated into outer and inner cortex. The outer cortex consists of aerenchyma having many air-cavities separated by one-celled thick septa.

The stele is protostelic with diarch and exarch xylem. The xylem has two large metaxylem elements at the centre and protoxylem elements at each end towards the periphery. Phloem bands are present on either side of Fig. 7.118 : Marsilea minuta. T.S. of petiole the xylem.

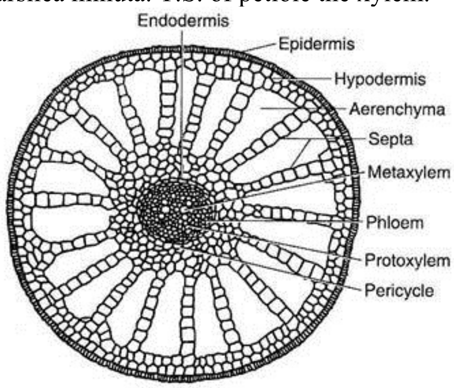

Fig. 7.118 : *Marsilea minuta*. T.S. of petiole

The stele is protostelic, generally triangular in outline and is externally bounded by endodermis. A single-layered pericycle is present just inside the endodermis.

The xylem is mesarch, consists of two outwardly curved strands. Protoxylem patches are present at both the ends with one or more metaxylem in the centre. The xylem is surrounded by phloem. Pith is absent.

The vertical section of the leaflet shows epidermis, stomata, mesophyll and vascular bundles. Stomata are present in the upper epidermis (in submerged species) or on both the upper and lower epidermis (in terrestrial and amphibious species).

Mesophyll tissue is differentiated into palisade and spongy parenchyma and generally associated with vertical airspaces. The vascular bundles are concentric with a central core of xylem surrounded by phloem. Each vascular bundle is separated from the mesophyll tissue by a layer of endodermis.

3. Root:

The primary roots are short-lived (ephemeral) and are replaced by adventitious roots. Roots usually arise at nodes on the lower side of the rhizome. However, in some species (e.g., M. aegyptiaca) the roots arise from the internodal region of the rhizome.

In transverse section, the root shows three distinct regions : the epidermis, the cortex, and the stele (Fig. 7.119). The epidermis is composed of single-layered parenchymatous cells, outer walls of which are thickly cuticularised. The cortex is differentiated into three zones, viz., the outer cortex, the middle cortex, and inner cortex. The outer cortex is aerenchymatous with many air spaces separated by radially elongated septa. The middle cortex is parenchymatous. The inner cortex is thick-walled, sclerenchymatous, internally bounded by the successive layers of endodermis and pericycle.

Reproduction in Marsilea:

Marsilea reproduces vegetatively as well as by means of the spores.

i. Vegetative Reproduction:

Under some unfavourable circumstances the subterranean branches of the rhizome form tubers. These structures have reserve food in the form of oil globules which help them to overcome the unfavourable conditions. On return of the favourable conditions, these tubers germinate and form new plant body (e.g., M. hirsuta, M. minuta, M. erosa).

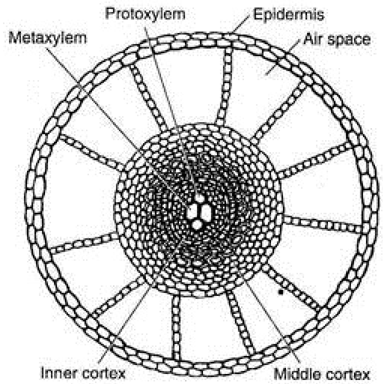

Fig. 7.119 : *Marsilea minuta*. T.S. of root

ii. Reproduction by Spores:

Marsilea is a heterosporous fern. It produces two types of spores i.e., the microspores and the megaspores. The microspores and megaspores are produced in microsporangia and megasporangia, respectively, and the sporangia are enclosed in special bean-shaped structures called sporocarps.

When young, the sporocarps are soft and green, but turns dark brown and hard at maturity. Sporocarps withstand desiccation and are reported to be viable even after twenty to twenty five years.

The sporocarp develops at the short branch of petiole called pedicel or stalk. In most species they occur singly, but in some species the number varies from two to twenty (Fig. 7.120).

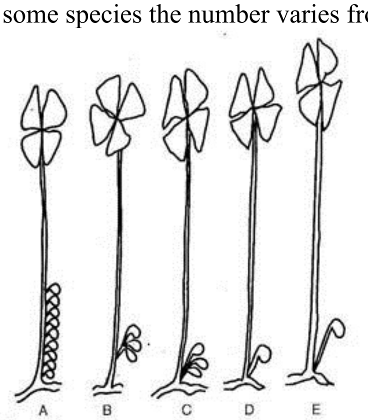

Fig. 7.120 : *Marsilea* : Attachment of sporocarps in various species. A. *M. polycarpa*, B. *M. quadrifolia*, C. *M. minuta*, D. *M. coromandelica*, E. *M. uncinata*

The mode of attachment of sporocarps with the petiole is of following types:

(a) Sporocarps are attached to one side of the petiole in a single row e.g., M. polycarpa, M. caribaca, M. subangulata, M. detlexa.

(b) Pedicels of the sporocarps are fused in groups and then attached to the petiole by a common stalk e.g., M. quadrifolia.

(c) Pedicels of all the sporocarps remain free and are attached to the petiole at a single point (e.g., M. minuta).

(d) A single sporocarp attached to the base of the petiole by the pedicel (e.g., M. coro- mandelica, M. uncinata).

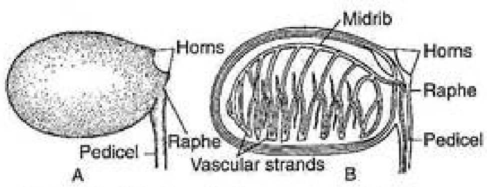

Fig. 7.121 : *Marsilea* : A. A sporocarp, B. L.S. of sporocarp showing vascular strands on one valve

The place of attachment of the pedicel with the body of the sporocarp is known as raphe (Fig. 7.121 A). The distal end of the raphe in some species is marked by the presence of one or two protuberances or teeth-like projections known as horns or tubercles.

The sporocarp wall is hard, thick, thus resistant against mechanical injury. Anatomically, the wall is differentiated into three layers. The outer layer is epidermis made up of single-layered cuboidal cell with sunken stomata.

The middle layer is made up of radially elongated compactly arranged thick-walled palisade cells. This is followed by second palisade layer which is comprised of more elongated thin-walled palisade cells.

A vertical longitudinal section (VLS) in the plane of the stalk shows that a single strong vascular strand enters the sporocarp near the lower horn (Fig. 7.121B) and continues forward all along the dorsal or upper side of the sporocarp thus forming a midrib (dorsal bundle).

From this midrib, the lateral side branches (lateral or commissural bundles) arise which eventually pass on to the two sides of the sporocarp. The sporocarp, therefore, has a bivalved structure.

Another bundle called placental bundle develops from the point of forking of lateral bundle which enters into the receptacle bearing sporangia and dichotomises. Thus a closed network of vascular system is formed within the sporocarp.

A vertical longitudinal section (VLS) of sporocarp away from the plane of the stalk reveals many sori arranged in vertical rows (Fig. 7.122). In this plane of section either megasporangia or microsporangia are visible. Each sorus is surrounded by an indusium. The development of sori is of gradate type. The gelatinous mucilage ring is more prominent in dorsal side.

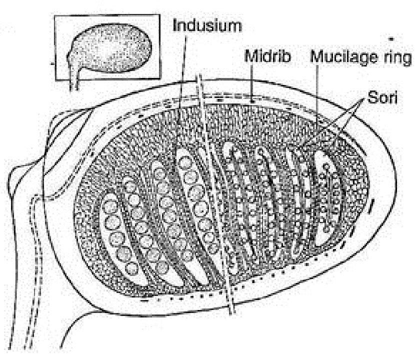

Fig. 7.122 : *Marsilea* (vertical) L.S. of sporocarp

A horizontal longitudinal section (HLS) cuts each sorus transversely and it is seen that each sorus is an elongated structure, covered by a delicate indusium.

The sori are gradate, basipetal in arrangement with a row of largest sporangia (megasporangia) at top and two rows of smaller sporangia (microsporangia) on two sides (Fig. 7.123). The mucilage ring is present in the form of two masses, one in the dorsal and the other in the ventral sides.

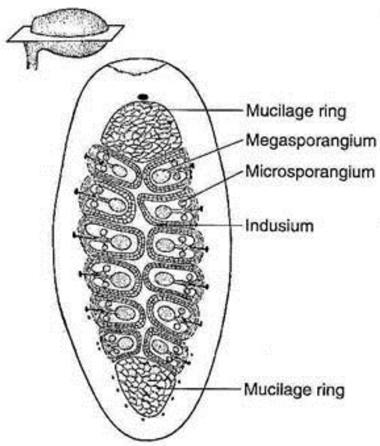

Fig. 7.123 : *Marsilea* (horizontal) L.S. of sporocarp.

A vertical transverse section (VTS) of the sporocarp shows only the sori on two sides (Fig. 7.124). Both the sori contain megasporangia if the section is taken through the megasporangia or the sori contain only microsporangia if it is taken through the microsporangia. The sporophore is seen in the form of two masses on either side. The mucilage ring is present only on the dorsal side.

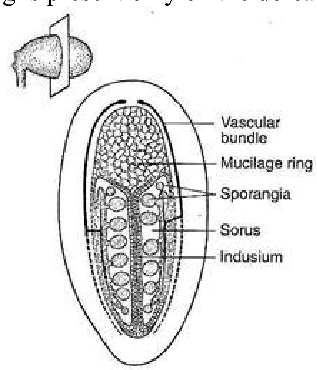

Fig. 7.124 : *Marsilea* (vertical) T.S. of sporocarp

Development of Sporangium:
Sporangial development is of the leptosporangiate type. The development of both the micro- and megasporangia is almost alike. The sporangial initials for megasporangium and microsporangium are formed at top and at the sides of the receptacle, respectively.
The initial cell divides periclinally (transversely) into an outer and an inner cell. The inner cell doe^ not take part in further development. The outer cell undergoes three successive diagonal divisions and forms a tetrahedral apical cell with three cutting faces.
This apical cell cuts off two segments along each of its three cutting faces which forms the stalk of the sporangium. Now the apical cell divides with the help of an arched periclinal wall towards its outer face and forms an outer jacket initial and an inner tetrahedral archesporial cell. The outer jacket initial divides anticlinally to form a single-layered jacket.
The archesporial cell divides periclinally to forms an outer tapetal initial and an inner primary sporogenous cell. Anticlinal and periclinal divisions of the tapetal initial forms a two-layered thick tapetum.
The primary sporogenous cell divides to form a mass of either 8 or 16 spore mother cells. Spore mother cells (2n) undergo meiotic division to form 32 or 64 haploid spores (n). The developments of both the sporangia are similar up to this stage.
In megasporangium, only one megaspore survives to become a large functional megaspore, while all the microspores are functional in microsporangium.
Opening of the Sporocarp:
The sporangium wall of Marsilea shows no sign of cellular specialisation (e.g., formation of annulus) required for dehiscence of sporangium. A sporocarp is a hard structure and it does not open until two or three years after their formation. This delay is probably due to the imperviousness of the hard sporocarp wall.

Hence the sporocarp may remain viable for even 50 years. The tissues slowly swell up by absorbing water in natural conditions. Thus the swelling puts pressure on the wall of the sporocarp and eventually it splits open along its ventral side into two halves.

Splitting is followed by the emergence of a long, worm-like gelatinous structure to which the sori are attached (Fig. 7.125). The mucilaginous cord may became ten or fifteen times larger than the sporocarp. Following the release of the sori from the sporocarp, the indusia and the sporangial wall disintegrate and the spores are liberated.

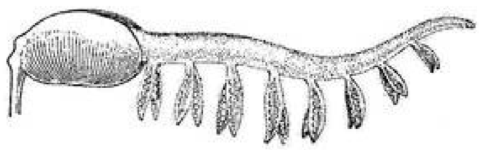

Fig. 7.125 : *Marsilea* : Extrusion of the sori on the mucilaginous cord

Gametophyte:

Marsilea is heterosporous i.e., they produce microspores and megaspores which eventually germinate to form the male and female gametophytes, respectively.

Male Gametophyte:

The microspores are small, globose structures with a thick outer ornamented exine and inner thin intine. The outer exine is covered by a thin layer called perispore. The microspore contains a distinct haploid nucleus and its cytoplasm is rich in starch grains.

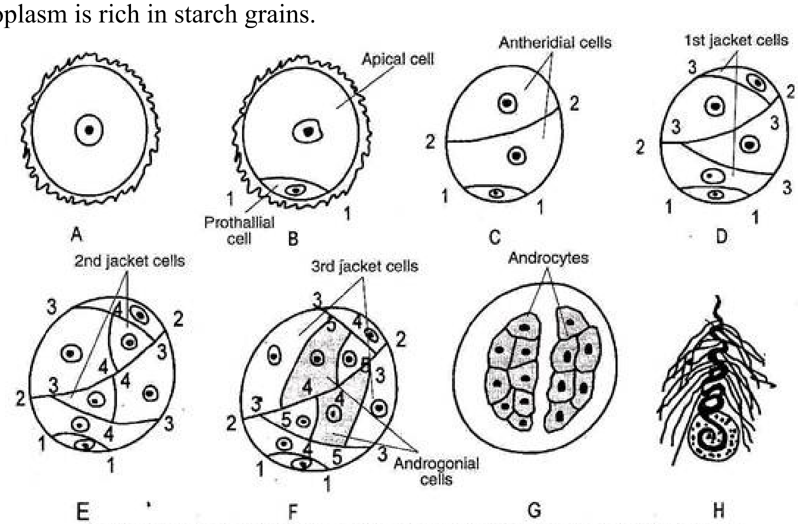

Fig. 7.126 : *Marsilea* : A–G. Stages in the development of male gametophyte, H. A sperm

The microspores germinate inside the spore wall (endosporic type) almost immediately after its release (Fig. 7.126A-G). It divides asymmetrically to form a small prothallial cell and a large apical cell (1-1). A division (2-2) of apical cell diagonal to prothallial cell forms two antheridial cells.

Then both the antheridial cells divide diagonally (3-3) with curving wall forming the first jacket cell and large wedge-shaped cell. The jacket cells do not divide, but the wedge-shaped cell divides periclinally (4-4) to form smaller inner cell (2nd jacket) and a large outer cell. Further, the periclinal division (5-5) of outer cell forms 3rd jacket and primary androgonial cell.

At this stage the male gametophyte consists of one prothallial cell, 6 jacket cells and 2 androgonial cells. After several divisions of the primary androgonial cells, sixteen androcytes are formed surrounded by jacket cells.

Later the prothalial cell and the jacket cells disintegrate and the two groups of androcytes, representing the two antheridia, float freely in the cytoplasmic mass within the original spore wall. Each androcyte becomes a motile antherozoid by dissolution of the androcyte membrane.

The antherozoids are corkscrew-shaped, multiflagellate structure characterised by the presence of a large posterior cytoplasmic vesicle (Fig. 7.126H).

Female Gametophyte:

The megaspore is an oval or elliptic structure, the wall of which imbibes water and expands to form a gelatinous mass around the megaspore. The spore wall expands to form a small papilla (protuberance) at the apical end where the nucleus is located in a dense part of cytoplasm. The remaining portion of the spore is filled with a frothy cytoplasm full of starch grains (Fig. 7.127A).

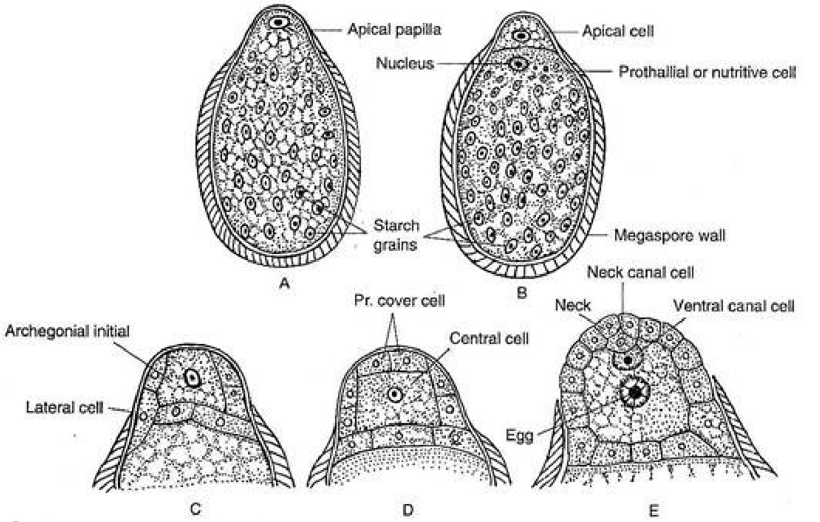

Fig. 7.127 : *Marsilea* megagametophyte : A. Megaspore, B–D. The stages in the development of megagametophyte, E. A mature archegonium

The first division in the apical nucleus of the large megaspore is transverse, forming a small nipple-shaped apical cell and a very large basal nutritive or prothallial cell (Fig. 7.127B). The prothallial cell provides the nutrition to the growing female gametophyte.

The apical cell further divides by three intersecting vertical walls to establish an axial cell surrounded by three lateral cells (Fig. 7.127C). Now the axial cell functions as archegonial initial which divides periclinally to form an outer primary cover cell and an inner central cell.

A small neck (2 tiers of 4 cells each) is derived from the primary cover cell. The central cell divides transversely to form an upper primary canal cell (behaves as neck canal cell) and lower primary venter cell (Fig. 7.127D, E).

The primary ventral cell again divides transversely to form a ventral canal cell and an egg. The growth of the archegonial complex ruptures the megaspore wall at the apical end and forms a conspicuous gelatinous mass with funnel-shaped papilla or protuberance. Now, the megaspore splits through the triradiate fissure and archegonium becomes exposed.

Fertilisation disintegration of the neck canal cell and ventral canal cell create a passage for the antherozoids to fertilise the egg. The antherozoids, after liberation from ruptured male gametophyte, enter through the gelatinous protuberances and moves downwards to the archegonium. One of the antherozoids eventually fuses with the egg to form a diploid zygote.

New Sporophyte (The Embryo):

The zygote is the mother cell of the next sporophytic generation. The first division of the zygote is vertical (in relation to the neck of the archegonium) followed by a transverse division resulting in the quadrant stage (four-celled stage) of the embryo (Fig. 7.128A, B). Subsequent development of the upper two cells forms the root and leaf, whereas the lower two cells give rise to the foot and shoot apex (Fig. 7.128C, D).

With the development of the embryo the vegetative cells of the surrounding gametophyte divides periclinally and form a two- to three-layered sheath (calyptra) around the embryo. The primary root grows vertically and establishes the sporeling in the soil. The young sporophyte has a well-developed primary root and leaf.

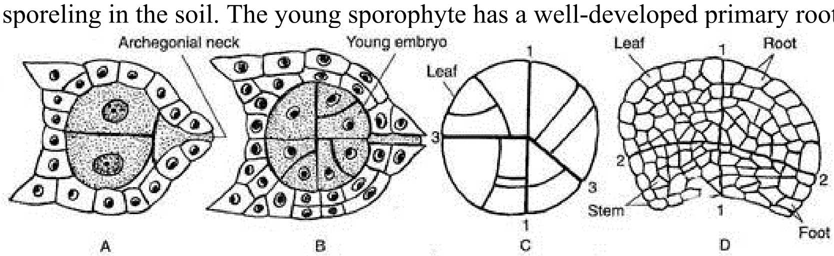

Fig. 7.128 : *Marsilea* : A–D. The stages in the developmen of embryo

The life cycle of Marsilea is shown in Fig. 7.129.

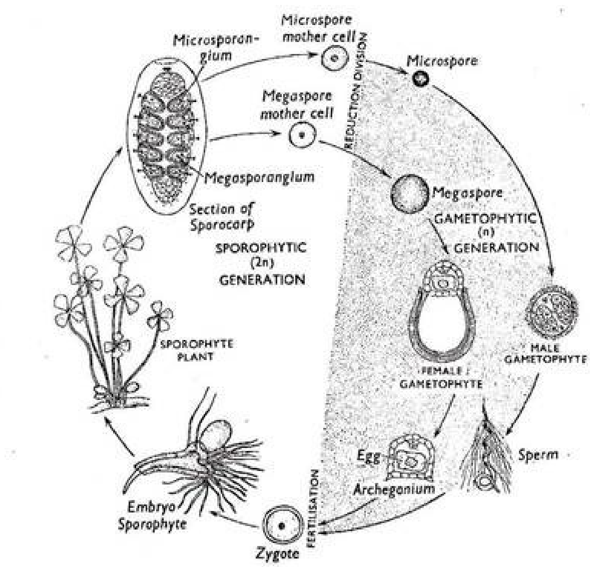

Fig. 7.129 : Life cycle of *Marsilea*

Morphological Nature of Sporocarp:

The morphological nature of the sporocarp of Marsilea has been controversial. There are three views which can be grouped under the following categories :

(i) Leaf segment theory or Laminar hypothesis,

(ii) Whole leaf theory or Petiolar hypothesis,

(iii) A phylogenetically synthesised new organ.

(i) Leaf Segment Theory or Laminar Hypothesis:

On the basis of the vascular supply to the peduncle as well as within the sporocarp, this structure has been considered to be a modification of a leaf segment rather than an entire leaf. This hypothesis was supported from time to time by a number of scientists. Although the scientists equated sporocarp with the lateral fertile part of a leaf, they differed on the number of pinnae involved and their mode of transformation into the sporocarp.

The Various Views:

According to Russow (1872), the sporocarp is made up of two leaflets and their ventral surfaces containing sori are facing each other.

Bower (1889) interpreted sporocarp to be a modified unipinnately compound leaf with rachis bearing two rows of pinnules which fused laterally to form sporocarp (Fig. 7.130A, B).

According to Campbell (1892) the sporocarp is a folded pinnately compound leaf where pinnae are fused to form the sporocarp.

Eames (1936) equated the sporocarp with the tip of the leaf whose margins bend downwards (Fig. 7.130C-D). A wing-like shoulder develops that protects the sori. The similarity between the course of vascular traces in the sporocarp and the vasculature of the leaf is an evidence in support of Eames' hypothesis.

According to Smith (1955) the sporocarp is a modified pinna with two abaxial sori. The infolding of the tvyo edges of the pinna with abaxial sori along the midrib forms the sporocarp. In the axil of each receptacle a flap-like indusium is formed (Fig. 7.130E).

Puri and Garg (1953) interpreted the sporocarp as a modified single leaflet in which the number of pinnules corresponds to the number of lateral bundles in the sporocarp (Fig. 7.130F).

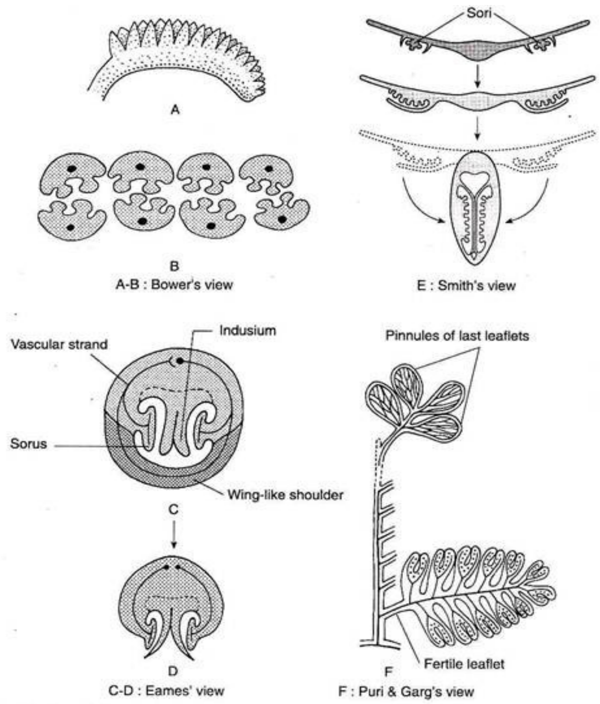

Fig. 7.130 : *Marsilea* : Morphological nature of the sporocarp (various views) : A–B. Bower's view, C–D. Eames' hypothesis, E. Smith's interpretation, F. Puri and Garg's hypothesis

(ii) Whole Leaf Theory or Petiolar Hypothesis:

Johnson (1933) is the proponent of this theory. According to this hypothesis, the sporocarp is the modification of the whole leaf (lamina and petiole) where the marginal cells of the leaf develop into sporangia instead of leaflets. Evidence in support of this hypothesis is derived from the development of secondary and even tertiary sporocarps on peduncle of primary sporocarp.

(iii) A Phylogenetically Synthesized New Organ:

Bierhorst (1971) interpreted the sporocarp of Marsileaceae to be a phylogenetically synthesized new organ which changed its morphological nature in mid-ontogeny. According to Bierhorst the sporocarp originates after the vegetative pinnae are formed. Each sporocarp arises from a single initial with three cutting faces, a condition unknown for any other fern pinna.

In the early stages of development, the marginal series of sporocarp initials are comparable to the sporangial stalk initials of ferns. Thus, there is a differential expression of genome where sporangial ontogeny is expressed in early stage and pinna ontogeny in later stage.