SPOROGENESIS IN *ISOETES TAIWANENSIS* DEVOL

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Abstract: The development of sporangium and sporogenesis in *Isoetes taiwanensis* DeVol are described. Based on cell lineage and cytoplasmic contents, the sporangium in *I. taiwanensis* is suggested to be of hypodermal origin. The ontogeny of microsporangium and megasporangium are the same in the early stage. The first indication of the young microsporangium is the differentiation of the irregular groups of deeply-staining cells (microsporocytes) and lightly-staining cells (which become trabecula, tapetum and part of sporangial wall), whereas the earlist indication as a megasporangium is the enlargement of the megasporocytes. The first fruiting leaves in the growing season are always megasporophylls, and then followed by microsporophylls. There is occasionally some irregularity in the order of succession, and sometimes a sporangium is found bearing both micro- and megaspores.

INTRODUCTION

The development of sporangium in *Isoetes* has been investigated in several species (Bower, 1894; Farmer, 1890; Goebel, 1880–1881; Hegelmaier, 1872; Hofmeister, 1862; and Smith, 1900). In an earlier observation on *I. lacustris*, Hofmeister (1862) mentioned that the sporangium proper and velum were of different origin, whereas Goebel (1880–1881) pointed out that these two structures have their common origin in the same species. However, the majority of later workers agreed with the observation that they originated from a group of common initial cells (Bower, 1894; Smith, 1900). These botanists have been more interested in detailing the mode of the formation of both the fertile part (sporocytes) and the sterile part (trabecula and tapetum). There are also some different views in their descriptions. These workers differ in their opinions regarding some aspects of the origin of the related structures and of eusporangiate in origin. The sporangium of *Isoetes* is massive and large, it arises from a group of superficial cells on the adaxial side of the leaf base.

Almost all botanists consider that *Isoetes* belongs to the heterosporous Lycopods, and that the microspores and megaspores occur in the separate sporangium, i. e. the microsporangium contains microspores and megasporangium contains megaspores. There are only two types of sporangia (Foster and Gifford, 1974). The sporangia of *I. taiwanensis* are very often found to contain both microspores and megaspores (DeVol, 1972). These are named mixed sporangia. A few other members of *Isoetes* are found to have mixed sporangium (Alston, 1959; Arnold, 1958; Goswami and Arya, 1968, 1970; and Smith, 1900), but this is extremely rare further detailed description concerning the mixed sporangia are in their reports.

Although this research was initiated as a traditional examination of the micro- and megasporogenesis in *I. taiwanensis*, the results also seem relevant to the ontogeny and some aspects of their related structures.

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MATERIALS AND METHODS

Isoetes taiwanensis DeVol was collected from Chi-hsin Mt. (七星山), and moved to water tanks in the shadding house in The Department of Botany, National Taiwan University. The plants were potted and submerged in the tanks with slowly running water for at least six months before the collection for sectioning.

The corms of about 1.5 cm in diameter were harvested twice each month on 15th and 30th from September, 1980, through February, 1982. Two corms were obtained each time. All the sporophylls used for fixation were limited to the leaf base bearing the ligule, velum, sporangium and a portion of the corm apex. The materials were fixed in FAA (Johansen, 1940), dehydrated, and run through the TBA-series to paraffin. Serial transverse and longitudinal sections were cut at the thickness of 8–10 μm and stained with Safranin, orange G, and tannic acid iron alum (Sharman, 1943), or Heidenhain's hematoxylin (Johansen, 1940). The material for the detection of insoluble carbohydrates was with Periodic acid-Schiff's reagent (Jensen, 1962).

RESULTS

Three types of the sporangia viz. microsporangium, megasporangium, and mixed sporangium, are recognized in *I. taiwanensis*. The microsporangium contains microspores, the megasporangium contains megaspores (Figs. 1–5). The megaspores in mixed sporangium are slightly smaller than those in the sporangium containing ony megaspores, and the microspores in the mixed sporangium are much smaller than in the sporangium containing only microspores. The microspores and megaspores in the mixed sporangium develop respectively into the functional microgametophytes and megagametophytes when cultivated in ⅔ strength of Hoagland solution.

The leaf initiation starts with periclinal cell divisions in a small group of both epidermal and subepidermal cells on the sides of the shoot apex. This group of cells continues to divide, forming a protruding leaf primordium (Fig. 6). This leaf primordium will develop into the leaf, ligule, velum, and the sporangium (Figs. 6–18). Therefore, this leaf primordium is actually a primordium of leaf-velum-sporangium complex. As it becomes a few cells high, one of the surface cells becomes enlarged and undergoes a series of cell divisions, finally giving rise to the ligule (Figs. 7–11). The detailed sequential stages in ligule formation in *I. taiwanensis* have been described by Yang (1973). The cells in the complex primordium on the abaxial side more frequently than those located on the adaxial side, and become more or less cylindrical structures by extension of the future leaf blade (Figs. 7–17).

The initiation and early development of the sporangium

Microsporangia and megasporangia are indistinguishable during the early stage of development. When the young ligule is still a few cells in length, a group of single-layered cells in the surface of the adaxial side of the complex primordium undergo the periclinal cell division and function as velum-sporangium primordium (Figs. 7–9, 44a). Apparently the velum and sporangium originate from a group of common cells (Figs. 10–15). The cells in velum-sporangium primordium are darkly stained (Fig. 12). Shortly after the first periclinal division takes place, a few cells located immediately below the ligule divide, becoming protruded in an upward oblique direction to give rise to the velum (Figs. 12-15, 44d). The margin of velum towards the ligule grows less than its opposite side. The velum reaches its final size earlier than the stage one of what is able to discern between microsporangium and megasporangium. As the velum grows, the remaining cells which are derived from the
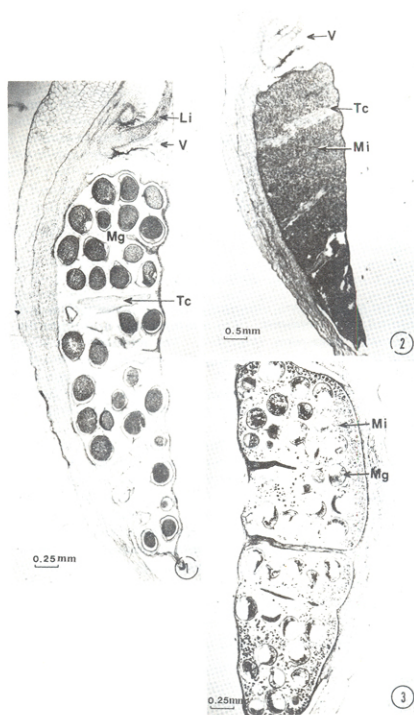
Figs. 1-3. Median longisection of sporophylls through the sporangium: (1) megasporangium; (2) microsorangium; and (3) mixed sporangium. Key to labeling refering to p. 85.
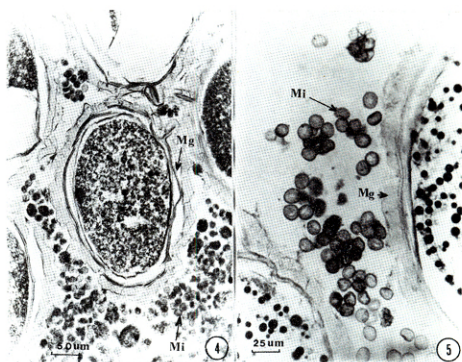
Figs. 4-5. Enlarged view from Fig. 3, showing both micro- and megaspores inside the mixed sporangium.

superficial cells after the first periclinal division follow a series of cell divisions to give rise to the sporangium. After the first periclinal division, the cells in outer layer divide anticlinally and the cells in inner layer divide in several directions. The former divides mainly in an anticlinal direction to become the epidermal layer of the sporangium (Figs. 17–19). Occasionally, they divide periclinally to increase the cell layer in the epidermis (Fig. 18). The epidermal layer is discernible from the inner cells by cell lineage in the early stage of development and by both cell lineage and lighter cellular contents in the later stage (Figs. 14, 17–23). They become lighter in cell contents in the later stage of development (Figs. 17–23). This distinctive appearance of epidermal layer persists for very long time, even in the stage of spore maturation (Fig. 29). As seen in Fig. 18, the cells which are derived from the inner layer after the first periclinal division appear to be darker in the cytoplasmic inclusions. But when stained with PAS reagent, both the epidermal layer and the inner cell group are identical (Figs. 14, 17). No apparent difference can be seen in total carbohydrates between them. The cells derived from the inner layer ultimately become trabecula and tapetum.

Microsporogenesis

The first indication which the microsporangium is the differentiation of the irregular groups of deeply-stained and lightly-stained cells. The former is the fertile region and the latter the sterile region which transverses the former (Figs. 20–22). The sterile region does not however, divide the fertile region into complete chambers. The cells in the fertile region finally become the microsporocytes, and those in sterile regions form the inner part of the sporangial wall, tapetum and trabecula. After the differentiation of fertile and sterile regions, the young microsporangium continues to enlarge in size, and the cells in it continue to divide. The cells in fertile regions retain their darkly stained appearance all the time
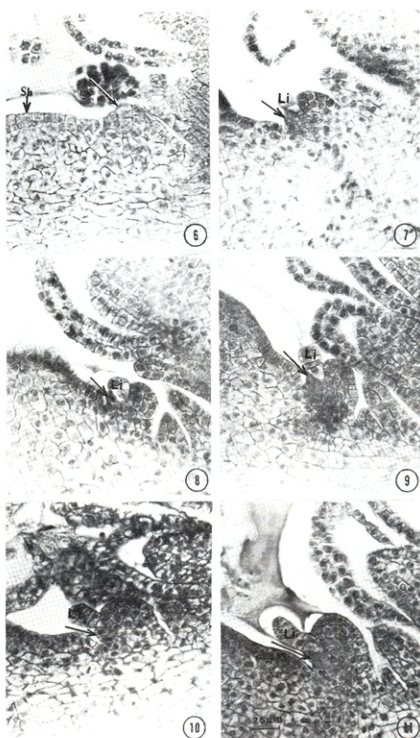
Figs. 6–11. Longisection of corm through the periphery of apical zone, showing the early stage of the sporangial development and its adjacent area.

Fig. 6. The initial of blade-ligule-velum-sporangium complex (arrow) in the side of shoot apex (sh).

Figs. 7–9. Showing a single row of velum-sporangium primordium (arrows) in the superficial layer beneath the young ligule.

Figs. 10–11. Arrows show the superficial cells located below the young ligule become more dense in cytoplasm.
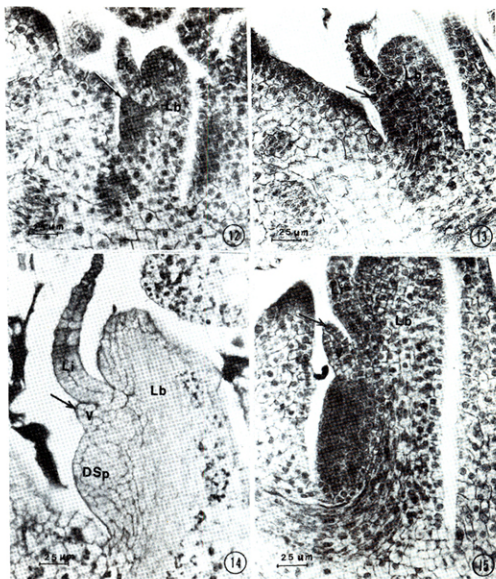
Figs. 12-15. Median longitudinal sections of young sporophylls showing various stages of the developing sporangia. Arrows show the upper part of superficial cells giving rise to the velum. (Fig. 14. Stained with PAS reagent.)

and become the microsporocytes (Figs. 22, 23). The microsporocytes as well as their nuclei pass through a period of resting and enlargement. The nuclei increase in size and become rich in chromatic substance (Fig. 23). Subsequently the microsporocytes separate from each other and also from the cells in the sterile region, i. e., tapetal cells (Figs. 24, 25). Shortly after the separation, the microsporocytes become round (Fig. 26) and follow the meiotic division. The meiotic division is synchronous and is of the successive type, i. e., the first division of the nucleus is followed by the formation of a cell wall before the next division of the daughter nuclei. Almost all of the microsporocytes undergo meiotic division and give rise to the microspores. The arrangement of tetrads is decussate shape. They have
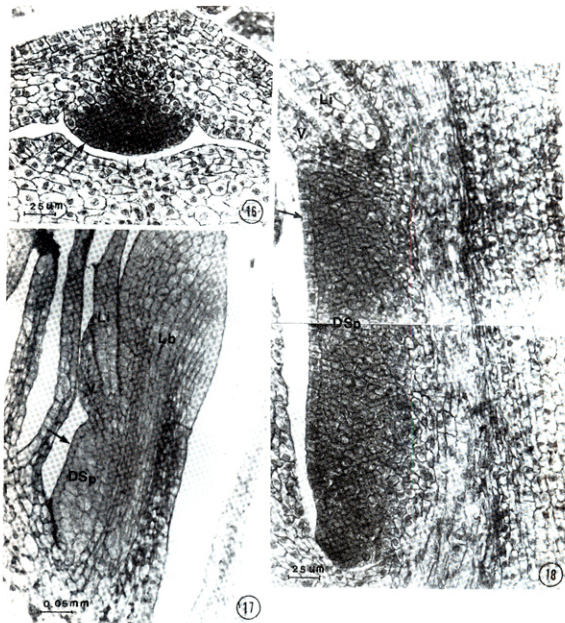
Figs. 16-18. Both transection (16) and Longisection (17, 18) through the developing
sporangia, showing the differentiation of epidermal layers (arrows).
(Fig. 17. Stained with PAS reagent.)

their walls in two planes at right angles (Fig. 27). The young tetrads soon fall apart.
The individual microspore is bilateral in shape (Figs. 28, 29).

The differentiation of tapetum in the sterile region occurs almost at the same time as
the microsporocytes separate from the cells in the sterile region (Figs. 24, 25). Shortly after
the separation of sporocytes, the cells in the outermost layer of the sterile regions, which
were formerly in contact with the fertile region, appear to be more deeply stained and will

Fig. 19. Transverse sections of the developing sporangium with various cell divisions in the deriva-
tives of the inner cells.

Figs. 20-21. The sporogenous tissue becomes recognizable as a microsporangium by its differentiation
into irregular deeply-stained (fertile region) and feebly stained radial band (sterile region).

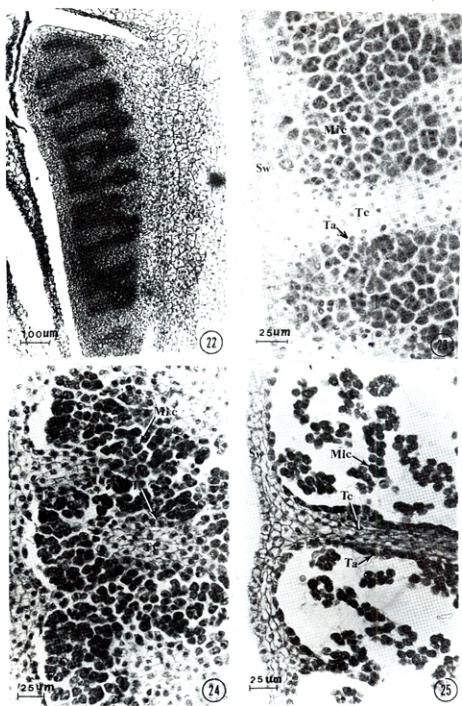25 um   DSp   ⑲

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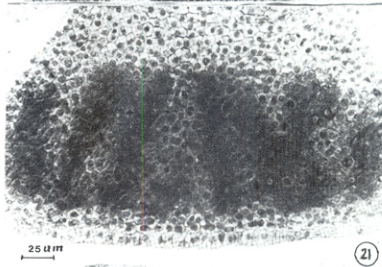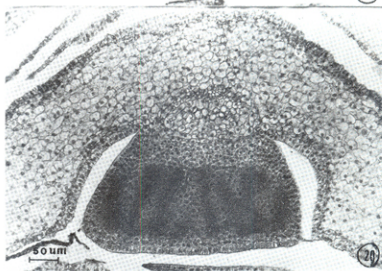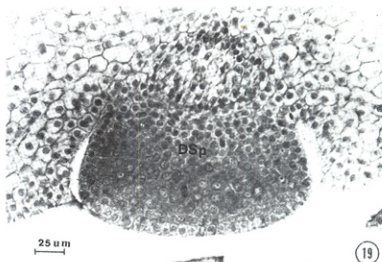
Fig. 22. Median longitudinal section of young microsporangium.
Fig. 23. Enlarged view of Fig. 22. Note the deeply-stained regions after a period of active
          multiplication, giving rise to the microsporocytes, and the feebly-stained regions
          giving rise to the trabecula, tapetum and sporangial wall.
Fig. 24. Showing the microsporocytes separate from sterile tissue.
Fig. 25. Showing that the trabecula cells are lengthened. The tapetal cells are more deeply
          stained and the individual microsporocytes fall apart,

become tapetum (Figs. 24, 25). The cells in this young tapetal layer multiply rapidly. They are frequently found in the process of mitotic division with the spindle axis perpendicular to either the surface of the sporangial wall or the inner cells of the sterile region. These inner cells of the sterile region will become trabecula. The mitosis in tapetum goes on for a rather long period until the sporocytes attain their final size and prepare for meiotic division. Consequently, the tapetal cells appear to be small and numerous. The tapetal cells are one layered in most areas, with two layers occuring in some places (Figs. 26, 29). The tapetum are recognizable even at the time when the microspores have matured (Fig. 28), but the outline as well as the stainiable nature of the tapetal cells become more obscure in the later stage (Fig. 29). As the microsporangia develop and increase in size, the cells of trabecula tend to elongate and slender in shape (Figs. 28, 29).

The cells in the sterile regions which lie toward the periphery of the sporangium and continuous with the epidermis of three to four layers form the inner part of the sporangial wall. So the sporangial wall is composed of one (occasionally two) epidermis which has derived from the outer layer formed soon after the first periclinal division. When stained with PAS reagent and KI-I$_2$ solution, there is an abundance of starch grains in trabecula and sporangial wall (Fig. 28).

Megasporogenesis

The first sign which leads one to recognize the early megasporangium differs very much from that in the young microsporangium. The early stage of development is the same as that in microsporangium (Figs. 44a-e). After the epidermal layer of the sporangial proper becomes identifiable by their cell lineage and the lighter-stained nature, certain cells in the inner region enlarge markedly (Figs. 30, 31). They are about four to five times larger than their neighbors. These enlarging cells are megasporocytes. The enlargement of the megasporocytes takes place during a considerable period before there is any possibility of distinguishing the trabecula. The enlarging megasporocytes do not lie in contact with one another (Figs. 30–32). They are separated from each other by the cells of ordinary size (Figs. 31–32). Soon after the megasporocytes reach their maximal size, the cells of three to four layers which are surrounding the megasporocytes increase in cytoplasmic density and will become tapetum (Figs. 32, 33). The remaining lighter stained region becomes the trabecula and a part of sporangial wall. The later stages of the formation of trabecula and sporangial wall are the same as those which occur in microsporangium. As the developing tapetum becomes denser in cytoplasmic contents, the tapetal cells gradually separate from the megasporocytes (Fig. 33). As a result of the separation of the tapetal layer from the megasporocytes as well as the growth of the whole sporangium, large sporangial cavities are formed surrounding the enlarging megasporocytes (Figs. 34, 44e). The tapetal cells are three to four layers in thickness. The tapetal cells located next to the sporangial cavity form outgrowing papilla which protrude into the cavity (Figs. 35, 39). The trabecula in megasporangia are fewer in number, but more massive as compared with those in microsporangia.

All the enlarging cells will give rise to megasporocytes. A thick callose wall is formed surrounding the megasporocytes prior to meiotic division (Fig. 36), and the indivisual megaspore in tetrads is also delimited by a wall with the same composition in the later stage of sporogenesis (Fig. 37). The meiosis in megasporocytes is the simultaneous type, ie, the nucleus of a megasporocytes continues with two successive divisions and cell walls are formed after the completion of meiosis (Figs. 37, 38). The tetrads are tetrahedral in arrangement. The further enlargement of the megaspores occurs after the tetrads formation. A mature megaspore is about 50 times larger than in the tetrads stage (Fig. 41). The
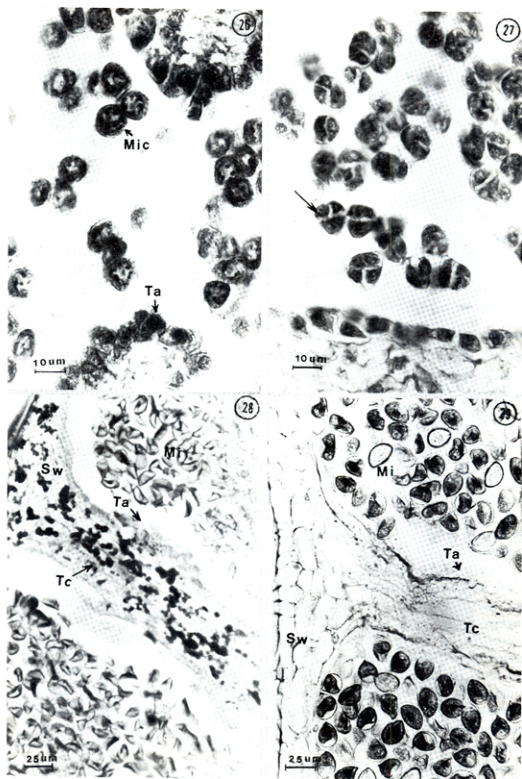
Fig. 26. The nuclei of microsporocytes increase in size, become rich in chromatin, and prepare to divide. At the same time, the tapetal inclusions continue to increase in density.

Fig. 27. Showing the tetrads arrange in typical decussate type (arrow).

Fig. 28. The young tetrads fall apart and become bilateral in shape. Note the presence of PAS granules in trabecula (in PAS stain).

Fig. 29. Microspores increase in size,
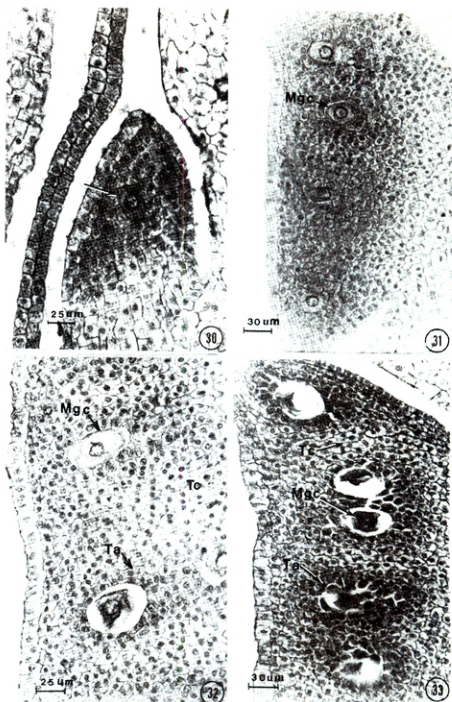
Figs. 30-33. Longisections of the young megasporangia showing the early stages of the megasporocyte formation.

Fig. 30. Enlargement of megasporocyte (arrow).

Fig. 31. Deeply stained area appears surrounding the enlarged megasporocytes (Mgc).

Fig. 32. The same stage of fig. 31, showing the deeply stained regions, which surround the megasporocytes, that will become tapetum. Feebly stained regions become the trabecula and a portion of sporangial wall.

Fig. 33. Tapetal cells become more conspicuous and separate from megasporocytes.
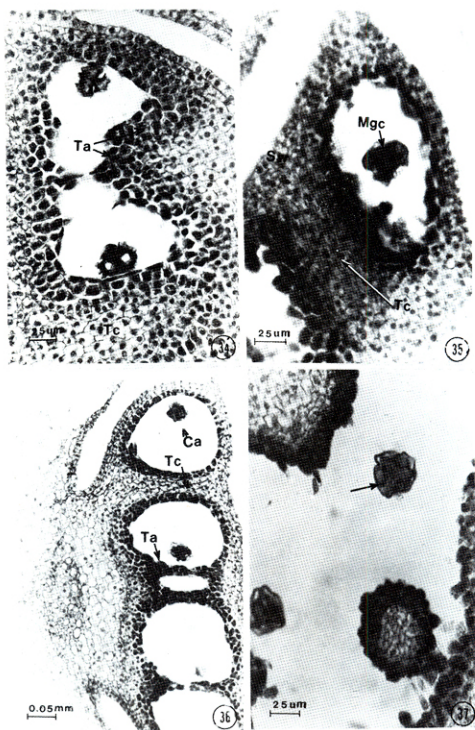
Figs. 34–36. Developing megasporangia, the cells of trabecula undergo elongation and
            flattening. Tapetal contents increase in density, and isolated megaspore
            mother cells become continuous by enlargement of cavities of sporangia
            and outgrowing tapetum.
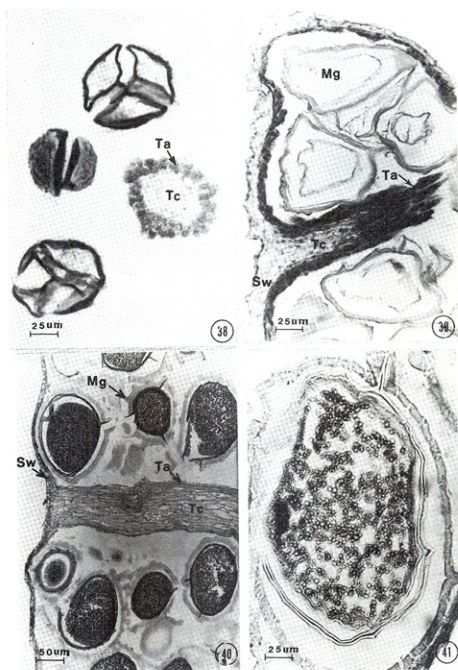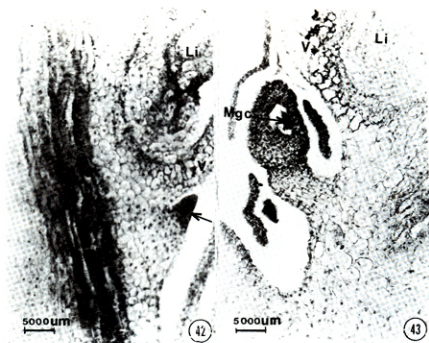Fig. 37. Showing tetrahedral division of megasporocytes (arrow).

Fig. 38. Showing tetrads split into four megaspores. Tapetum is still evident.
Fig. 39. Showing the young megaspores and papilla-like tapetum.
Fig. 40. Showing the mature megaspores and more elongated trabecula.
Fig. 41. Enlarged mature megaspore.

Figs. 42-43. Median longitudinal sections of aborting sporangia (arrow), showing the normal ligule and velum.

cytoplasmic contents of tapetal cells in the mature megasporangium are always denser than those found in the mature microsporangium.

Sterile sporangia

It is also a common case that aborted or undergrown sporangia are found present in association with so-called sterile leaves (Fig. 42). These sporangia are very small. As seen in longitudinal sections, they range from a few cells to several hundred cells when the associated lamina, ligules, and velums are fully expanded. Most of them are not detectable when examined under a dissecting microscope. The mature spores are occasionally found inside the aborted sporangia. Studying their mode of sporogenesis, it was found that they are megaspores rather than microspores (Fig. 43). However, these megaspores are always smaller than those obtained in the normal megasporangium.

Seasonal changes and arrangement of the sporangia

The sporophylls are arranged spirally and fit tightly together. There is no regular order in the distribution of sporangia within the corm. As shown in Table 1, corms may consist entirely of megasporangia, or of microsporangia, or of mixed sporangia. In mixed corms, some bear an outer megasporangial zone with an inner zone of microsporangia, and some in inverse situation, in which the two types of sporangia form irregularly mixed up. And still some other corms bear entirely sterile leaves. It is also shown in Table 1 that there is a slightly correlation between the appearance of the sporangia and the seasonal changes. Most corms which were collected after August and September have sporangia only in the very old leaves (located in the outermost layer of the corm). No corms with young leaves bearing sporangia were found until the collections were made the next February and March. Since the sporangia with their associated sporophylls are formed in a acropetal sequence, and have to hold onto the corms for rather long time after maturation, it is possible to trace the approximate time of the formation of a given sporangium.
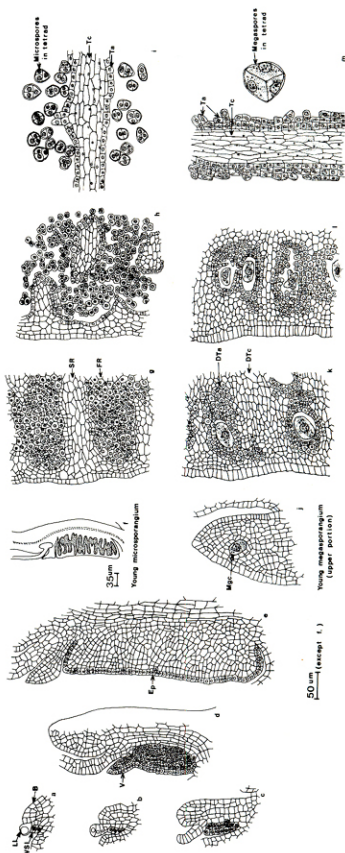
Fig. 44. Camera lucida drawings showing the development of sporangium. Refering to Figs. 7, 9, 12, 15, 23, 24, 30, 32 and 33.

Table 1. Seasonal changes of sporangial formation

Table 1: Seasonal changes of sporangial formation

Sequence of leaf counting from center of corm

———— : Sterile leaf and undifferented sporangia

+ : Microsporophyll   * : Heterosporous sporophyll

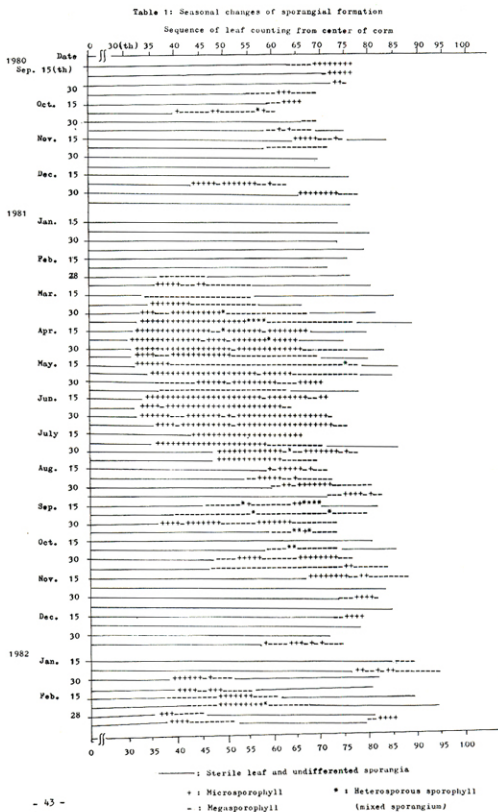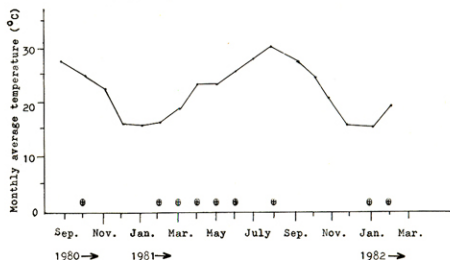– : Megasporophyll   (mixed sporangium)

Table 2. Graph showing the seasonal variation of the temperature and sporangial formation. ⊕ represents the presence of young sporangium

Therefore, it reveals that the fruiting period lasts from February to September.

The formation of the sporangia is also affected by temperature. As the temperature increases in late February, the young sporangia commence to form. When the temperature slowly declines at the end of August, the young sporangia gradually disappear (Table 2). The formation of megasporangia always precede microsporangia formation at the beginning of a growing season. The mixed sporangia are frequently found in the corms collected of either at the beginning or the end of the growing season (Table 1). It is a very sommon case for several mixed sporangia to be found born in the same corm. The appearance of mixed sporangia is very low in frequency as compared with that of both micro- and megasporangia. We examined 1,213 sporangia and found only 23 mixed sporangia (1.9%), 602 microsporangia (49.6%), and 588 megasporangia (48.5%). These results suggest that both micro- and megasporangia have almost the same frequency in the entire population. The aborting sporangia are not included in this counting.

Key to labeling

B	. . . . . . Blade primordium	Mgc	. . . . Megasporocyte
Ca	. . . . . Callose	Mi	. . . . . Microspore
DSp	. . . . Developing Sporangium	Mic	. . . . Microsporocyte
DTa	. . . Developing Tapetum	Sh	. . . . . Shoot apex
DTc	. . . . Developing Trabecula	SR	. . . . . Sterile region
Ep	. . . . . Epidermal layer	Sw	. . . . . Sporangial wall
FR	. . . . . Fertile region	Ta	. . . . . Tapetum
Lb	. . . . . Leaf blade	Tc	. . . . . Trabecula
Ll	. . . . . Ligule initial	V	. . . . . . Velum
Li	. . . . . . Ligule	VSl	. . . . Velum-sporangal initial
Mg	. . . . Megaspore		

DISCUSSION

As observed by most workers in *Isoetes* (Bower, 1894; Smith, 1900), both the velum and the sporangium have their common orgin in their early development in *I. taiwanensis*.

The velum is formed from a few cells located just below the ligule in the outer layer, which was formed after the first periclinal division in the velum-sporangium primordium. The velum is supposed to be the outer extension of the sporangial wall rather than the velum and sporangium being of different structure as mentioned by Bower (1894). It also agrees with Smith's (1900) suggestion that the velum might be considered as a sterilizing portion of the sporangium. The cell lineage and cytoplasmic contents in the epidermis of the sporangium appear to be very particular and distinct even in the very early stage of development (Fig. 13). The epidermis of the sporangia seems always to be neglected by most of the early workers (Bower, 1894; Farmer, 1890; Hofmeister, 1862; and Smith, 1900). But Hegelmaier (1872) considered that the outer layers which become the sporangial wall are from the beginning separated from the inner complex, so emphasized was the deep-origin of the sporogenous tissue. Goebel (1880-1881) employed the term "archesporium", which is in hypodermal position to designate as sporangial initial, and to demarcate from the superficial layer. The superficial layer indicated by Goebel (1880-1881) was actually the epidermal layer topographically. Evidently, the sporangia in *I. taiwanensis* are hypodermal in origin. The outermost layer of the sporangial wall is supposed to be the epidermis. The epidermis is uniseriate in the most areas, and biseriate in a few areas. It is also true that the sporangial wall in some gymnosperm members exhibit the epidermal layer rather than the wall cells derived from the sporangial proper (Erspamer, 1952; Singh, 1961; Singh and Chatterjee, 1963; Owens and Pharis, 1967).

The first indication to distinguish the microsporangia from the megasporangia in the early stage of development shows much similarity to that in several species of *Isoetes* studied by earlier workers (Bower, 1894; Foster and Gifford, 1974 Smith, 1900). It seems that the early stage of the differentiation between microsporangia and megasporangia in *Isoetes* does not vary among the plant species.

As that in the majority of heterosporous vascular plants, the megasporocytes are much larger than microsporocytes and much fewer in number. The enlargement of the megasporocytes is the earliest and the most conspicuous change inside the developing megasporangia of *I. teiwanensis*. There is no noticeable enlarging process in the microsporocytes inside the microsporangia. Both microsporocytes and megasporocytes separate from the sterile tissues (tapetum and trabecula) before the meiotic division. The separation of microsporocytes from the sterile tissue occurs almost at the same time as the differentiation of the tapetal cells, whereas the separation of megasporocytes occurs after the differentiation of tapetum (compare Figs. 22-24 and Figs. 31-33). The megasporangia always contain more cell layers of tapetum than the microsporangia, and the tapetal cells in megasporangia always become papillate, protruding into the sporangial cavities. Smith (1900) mentioned that some of the tapetal cells might be derived from the degenerating megasporocytes based on the presence the large amount of the tapetal cells in the megasporangia. The tapetal cells maintain their morphology up to the time of spore maturation. Goebel (1930) described that as the secretory type tapetum. Foster and Gifford (1974) also observed the presence of the degenerating megasporocytes functioning as nourishing tissue for megaspore development, as well as acting as plasmodial tapetum. But this situation seems not the case in the present investigation. No tapetal cells seem to be derived from the megasporocytes. All the enlarging megasporocytes undergo meiotic division and give rise to the megaspores. No plasmodial tapetum is found in the megasporangia, this is the same in the microsporangia. Though there were more than one type of tetrads arrangement in the same sporangium in some *Isoetes* species (Smith, 1900) only one type in each type of sporangium, i. e. decussate type in microsporangia, and tetrahedral type in megasporangia, was found in *I. taiwanensis*.

It was found that almost all of the leaves in some corms have sporangia. It seems

that all the leaves are potential sporophylls. Synchronous development of the sporocytes inside the large sporangia, the spiral arrangement of the leaves, and potential sporophylls of all leaves are all phenomena which suggest that this plant has probably retained a rather primitive nature of the sporophyte rather than the other living Lycopods.

The occurrence of two kinds of spores in the same sporangium is also seen in some other vascular plants such as: megasporangium of *Marsilea* (Pettitt, 1970); *Selaginella sulcata* (Pettitt, 1974, 1977); in ovules of Ginkgo (Stewart and Gifford, 1967); and *Encephalartos* (De Sloover, 1961). All of these are due to cytoplasmic gradients or chromosome inbalances in the sporocytes. These explanations seem not be the case in *I. taiwanensis*. Both microspores and megaspores in the mixed sporangia are always smaller than those obtained from the normally microsporangia and megasporangia. The sporadic occurrence of the mixed sporangia in *I. taiwanensis* suggests that this is a relict phenomenon. Unfortunately, we failed to obtain the complete series of specimens in the development of mixed sporangia.

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臺 灣 水 韭 的 孢 子 生 成

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摘　　要

　　此篇是描述臺灣水韭 (*Isoetes taiwanensis* DeVol) 的孢子囊發育和孢子生成過程。根據細胞的排列及細胞質形態，可以認爲臺灣水韭 (*I. taiwanensis*) 是起源自下皮組織 (Hypodermal origin)。小孢子囊和大孢子囊的早期發育很相似，形態上無任何差別，直到小孢子囊內部組織分化爲不規則深染色區 (即小孢子母細胞) 及淺染色區 (不孕性細胞區，如 trabecula、營養層和孢子囊壁) 而可辨別，此期在整個小孢子囊內之各種細胞之大小甚爲一致。但在大孢子囊內大孢子母細胞不斷增大至比鄰近細胞約四至五倍大，才可做辨別大孢子囊的指標。在一生長季中，其先形成的孢子葉，通常是大孢子葉，隨後才有小孢子葉，其泪長次序並不太規則，有時在同一孢子囊內同時具有大孢子和小孢子，但爲數甚少，約佔 1.9%。