Strobilar Organization in Philippine Species of *Selaginella*

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Received: August 20, 1992

ABSTRACT

This paper (1) describes for the first time the 12 types and subtypes of strobilar organization (based on sporophyll arrangement along the strobilar axis) found in 41 of the 50 Philippine species of *Selaginella* based on the microscopic analyses of more than 2,000 cleared strobili; (2) indicates the occurrence of these types and subtypes of strobilar organization in the various species; (3) discusses the value of strobilar organization in the taxonomy of the Philippine species vis-a-vis v A v R's system of classification; and (4) proposes and presents evidence for several pathways by which the presumed most specialized derived types of strobilar organization (Type IV: one which consists wholly or predominantly of microsporophylls and Type V: one which consists wholly or predominantly of megasporophylls) could be derived from the presumed basic type (Type 1a: one with a basal zone of megasporophylls + an apical zone of microsporophylls).

INTRODUCTION

Following the anatomical studies of several exotic species of *Selaginella* in the mid-1950s by one of us (Zamora 1958, 1959), work on the local species began in the mid-1960s and proceeded intermittently through 1990 (Zamora et al. 1967; Zamora 1971; Balagat 1971, Bagaoisan-Cosico 1972; Tan 1974, 1975; Price 1975; Mendoza and Zamora 1980, 1981; Tan and Jermy 1981; Zamora 1984, 1988; Mercado 1990) with the long term purpose of accumulating morphological and anatomical data to be used in monographing the genus *Selaginella* of the Philippines. As Alston (1935) has stated, the taxonomy of the Philippine species is far from satisfactory.

In 1935, Alston stated that the principal difficulty has been the large number of species described by Hieronymus (1901, 1913); many of these have been reduced to synonymy. In spite of this great reduction in the number of names, the process has not been carried far enough, as Alston has retained a number of somewhat dubious species. In this connection, Alston especially directed the attention of field workers to the large erect species (*S. magnifica, S. procera, S. elmeri, S. latifrons, S. agusanensis, S. copelandii, S. ramosii, S. neei, S. fenixii, S. jagorii, S. halconensis, S. aenea, S. presliana, S. luzonensis, S. flabelloides* and *S. cupressina*), where further material is most likely to lead to modification of the taxonomy of the genus.

Indeed, (1) *S. agusanensis* is doubtfully distinct from *S. latifrons* (Alston 1935, p. 378); (2) *S. copelandii* could also be said to be doubtfully distinct from *S. latifrons;* and (3) *S. flabelloides* is doubtfully distinct from *S. cupressina* (Alston 1935, p. 381). Already, Price (1975) has treated (1) *S. halconensis* as a synonym of *S. jagorii,* (2) *S. peltata* as a synonym of *S. involvens,* and (3) *S. biformis* as a synonym of *S. flagellifera.*

The aspect of the work under report pertains to the strobilar organization (based on sporophyll arrangement) of 39 species of *Selaginella* consolidated from Zamora (1971), Balagat (1971), Bagaoisan-Cosico (1972), Tan (1974), Tan and Jermy (1981), and Mercado (1990). Included here are information on strobilar organization of two species reported by Dahlen (1982, 1988). The 41 species covered in this paper represent 82% of the 50 species known from the Philippines; 17 of these are endemic (Table 1).

TERMINOLOGY

In *Selaginella,* the sporophylls (sporangia + foliar structures associated with the sporangia) are organized in definite strobili. They are arranged spirally around the strobillar axis but the spiral becomes so condensed that the associated leaves are disposed almost opposite to each other, in four distinct longitutidinal rows, the lower ones overlapping those immediately above (Mitchell 1910; Spangler 1937).

The foliar structures associated with the sporangia in a given strobilus may be of one form (i.e., monomorphic) or they are of two forms (i.e., dimorphic). A strobilus with monomorphic associated leaves is tetragonous, while one with dimorphic associated leaves is complanate or flattened (the larger leaves are on the upper side while the smaller leaves are on the lower side of the strobilus).

The sporangia are of two kinds: one kind produces smaller spores (microspores) and is termed microsporangium, while the other kind produces larger spores (megaspores) and is termed megasporangium. The microspores range in size from 15–20 microns (*S. luzonensis*; Knox 1950) to 58–70 microns (*S. tamariscina*, Tan 1974). The megaspores range in size from 150–200 microns (*S. intertexta*) to 650–700 microns (*S. opaca*; Tan 1974). The minimum size characteristic of modern spores bearing endosporic female gametophytes is 200 microns (Chaloner 1967; Andrews et al. 1974).

Development of the sporangia (based on *S. philippina*). The sporangia arise from one or a row of more than one superficial cells in the axil or just below the axil of the associated leaves. These superficial initials undergo periclinal divisions resulting in an outer tier of cells, the primary wall cells and an inner tier, the primary sporogenous cells. The primary wall cells undergo repeated anticlinal and periclinal divisions resulting in the formation of a two-layered sporangial wall. On the other hand, the sporogenous cells undergo periclinal divisions giving rise to an outer layer of cells which ultimately becomes the tapetum, and the inner cells which by anticlinal and periclinal divisions, produce the sporogenous tissue, these forming the potential sporocytes. The cells at the base of the developing sporangium that do not participate in the formation of the sporangium proper form the short stalk of the sporangium. In the sporangia that will produce microspores, a large proportion of the sporocytes functions as microspore mother cells and undergoes meiosis to form tetrads of microspores and a small proportion degenerates which together with the degenerative tapetal cells form a fluid medium in which the microspores float. In the sporangia that will produce megaspores, all the sporocytes but one usually degenerate. The one surviving sporocyte functions as the megaspore mother cell, undergoes meiosis to form a tetrad of megaspores. The degenerative sporocytes and the tapetal cells form a fluid medium and serve as source of nourishment for the developing megaspores. The megaspores enlarge enormously filling the cavity and distending the wall of the megasporangium.

The microsporangium + the associated microphyll is termed microsporophyll, while the megasporangium + the associated microphyll is termed megasporophyll. A given strobilus may contain (1) both kinds of sporophylls in varying proportions or (2) only one kind, i.e., microsporophylls only or megasporophylls only. It may contain (1) mature sporophylls (towards the basal region), (2) juvenile sporophylls (towards the apical region), and (3) sporophylls with non-developed (arrested) sporangia (in-

termingled with mature sporophylls) (Hieronymus 1901; Goebel 1905; Mitchell 1910; Sykes and Stiles 1910; Duerden 1929; Spangler 1937; Horner and Arnott 1963; Jermy et al. 1967; De la Sota and Morbelli 1981; Fraile and Riba 1981; Quansah 1988).

MATERIALS AND METHODS

The strobili used consisted of (1) dried (herbarium), (2) liquid-preserved, and (3) fresh specimens taken from various sources, thus: (1) dried materials were obtained from herbarium vouchers deposited at the Herbarium, Institute of Biology, College of Science, University of the Philippines, Quezon City (PUH); Philippine National Herbarium, National Museum, Manila (PNH); Herbarium, College of Agriculture, University of the Philippines, Los Baños (CAHP); Herbarium, College of Forestry, University of the Philippines (LBC); (2) liquid-preserved materials from the laboratory of one of us (PMZ); and (3) fresh materials from the Makiling National Park (Los Baños) and the UP-NSRI Fernery (Quezon City).

At least 10 strobili of each species were obtained from several geographic sources. These were prepared for microscopic analyses following the clearing technique and staining schedule of Zamora et al. (1967). The types and subtypes of strobilar organization for each species were determined with the aid of a stereoscopic dissecting microscope and a compound microscope.

Ordinarily, the kind of sporangium, whether megasporangium or microsporangium, can be told with ease even though its content is lost to dehiscence at maturity. The four large megaspores always deformed the larger megasporangium to become conspicuously lobed, while the microsporangium remains smaller and generally obovoid or reniform (Zamora 1971; French 1972). Yet difficulties were experienced in distinguishing the megasporangium from the microsporangium in *S. involvens* (*S. polyura, S. peltata*) and *S. flagellifera* (*S. biformis*). In both species, the megaspores are small and did not deform the megasporangium even at maturity. Thus, in these species, much time and effort were spent in locating intact strobili.

RESULTS AND DISCUSSION

Types and subtypes of strobilar organization. Based on the arrangement and distribution of sporophylls (microsporophylls, megasporophylls, non-developed sporophylls, juvenile sporophylls) along the strobilar axis, 12 types and subtypes of strobilar organization are recognized, as may be gleaned from

Table 2. Figure 1 is a graphical representation of said types. (As indicated in Figure 2, the two middle vertical rows of circles represent the two upper vertical rows of sporophylls in the strobilus. In planar position, these are continuous with the vertical row of median leaves on the stem. Hence, they are described as occupying the median plane of the strobilus. The other two vertical rows of sporophylls along the sides correspond to the lower vertical rows of sporophylls in the same strobilus [Figure 2] which are continuous with the lateral leaves of the stem and are therefore regarded as lateral in position. This appears to be a more accurate way of describing the position of the sporophylls in a strobilus because, in a platystichous strobilus, the two vertical rows of larger lateral sporophylls [not really lateral in orientation] are always seen in continuity with the median leaves of the stem, a condition termed "resupinate" by Aldewerelt [1915] and "having a 180° twist" by Jermy et al. [1967]. No satisfactory explanation of this interesting phenomenon has yet been proposed. Tryon [1955] suggested that it is an adaptation to protect the developing sporangia from possible external injury.)

Strobilar organization relative to v A v R's system of classification. Table 3 shows the number of strobili examined and the percentage of strobili exhibiting the types and subtypes of strobilar organization in the 41 Philippine species of *Selaginella* covered in this paper with v A v R's system of classification as framework. (In this paper, a particular pattern of strobilar organization is considered a major type if its percentage of occurrence is 45% and above, and thus, a pattern of strobilar organization is considered a minor type if its percentage of occurrence is below 45%, i.e., from 44 to 1%) The types and subtypes of strobilar organization found in the various species vis-a-vis v A v R's system of classification are indicated below:

Section Monostelicae

Subsection Homeostachys

Group Rosulantes. *S. tamariscina*, the only species in this group, is unique in that it exhibits the only type of strobilar organization, i.e., Type Ic, among the 41 species covered in this paper.

Group Decumbentes. There are no local representatives of this group in the country.

Group Radicantes. Two (*S. auriculata, S. negrosensis*) of the three species in this group exhibit a common type of strobilar organization, i.e., Type VIc, while the third species (*S. remotifolia*)

exhibits entirely different types of strobilar organization (Types Ia, Ia1).

Group Ascendentes. Nine (*S. agusanensis, S. alligans, S. copelandii, S. cumingiana, S. elmeri, S. fenixii, S. intermedia, S. jagorii, S. magnifica*) of the ten species covered in this group exhibit a common type of strobilar organization, i.e., Type VIb. The tenth species (*S. repanda*) shows quite a different major type of strobilar organization, i.e., Type V.

Group Caulescentes. The four species (*S. cupressina, S. involvens* (Alston 1937), *S. luzonensis, S. moellendorffii*) show various patterns of strobilar organization but all of them exhibit Types VIb or VIc or both. *S. involvens* is remarkable in that its major type of strobilar organization is Type Ib which it shares with *S. opaca* (Subsection Heterostachys, Group Bisulcatae).

Group Pubescentes. The two species (*S. flagellifera, S. uncinata*) both show Type IIIa. However, they differ from each other as follows: Type IIIa is the major strobilar organization for *S. uncinata* (Dahlen, 1982, 1988), while Type VIc is the major type of strobilar organization for *S. flagellifera.*

Subsection Heterostachys

Group Intertexta. While the five species in this group covered in this paper exhibit different major types of strobilar organization, three of them (*S. ciliaris, S. intertexta, S. nummularia*) have a common type, Type V.

Group Bisulcatae. The two species (*S. boninensis, S. opaca*) covered in this group have no type of strobilar organization in common.

Group Proniflorae. Dahlen (1982, 1988) reported that *S. heterostachys* exhibits Type IIIa as a major type of strobilar organization which type is also shown by several species in other groups.

Group Suberosae. Three (*S. aristata, S. llanosii, S. philippina*) of the five species exhibit the same major type of strobilar organization, i.e., Type V, while *S. eschscholzii* shows Type Ia1 and *S. myosuroides* shows Type IIIa as major type of strobilar organization. However, all the five species exhibit Types IV or V or both types.

Group Brachystachyae. Type IIIa is the major type of strobilar organization shown by the representative of this group, *S. ornata*, which is also shown by several species in other groups.

Section Pleiostelicae. Six (*S. delicatula, S. gastrophylla, S. lacerata, S. engleri, S. usterii, S. willdenovii*) of the seven species covered in this paper show common types (Types IV, VIa, VIc) as a major or minor type of strobilar organization. The seventh species (*S. plana*) shows no pattern; though this is the case, *S. plana* is thought to be rightly placed in this group because it too produces strobili with many microsporophylls and few megasporophylls.

It is clear from the foregoing account that all or most of the species that make up groups vis-a-vis v A v R's sytem of classification in those groups that are represented by more than one species show similar types of strobilar organization. Said similarities are here taken as indications of a taxonomic value of the character under consideration at the level of the group or section as was also indicated by Horner and Arnott (1963) for North American species, Fraile and Riba (1981) for Mexican species, and Quansah (1988) for African and Madagascan species. The type of strobilar organization can likewise indicate discrepancies in taxonomic placements of certain species in a system of classification, e.g., *S. remotifolia* may be misplaced in Group Radicantes, while *S. repanda* may be misplaced in Group Ascendentes (see Table 3).

Occurrence of major types of strobilar organization. Table 4 shows the number of species showing the 12 types and subtypes of strobilar organization in the 41 species of *Selaginella* covered in this paper. Although several species belonging to widely different groups in the Section Monostelicae exhibit Type Ia as a minor type of strobilar organization such as (1) *S. remotifolia* (Subsection Homeostachys, Group Radicantes), (2) *S. repanda* (Subsection Homeostachys, Group Ascendentes), (3) *S. intertexta* (Subsection Heterostachys, Group Intertexta), (4) *S. opaca* (Subsection Heterostachys, Group Bisulcatae), (5) *S. llanosii* (Subsection Heterostachys, Group Suberosae, and (6) *S. philippina* (Subsection Heterostachys, Group Suberosae), no species possesses this type as a major pattern.

Three types (Types Ic, II, VIa, including the 'no pattern' category) are characteristic major types of strobilar organization of each of the following species: (1) *S. tamariscina* (Section Monostelicae, Group Rosulantes) (Type Ic), (2) *S. negrosensis* (Section Monostelicae, Group Radicantes) (Type II), (3) *S. lacerata* (Section Pleiostelicae) (Type VIa), and (4) *S. plana* (Section Pleiostelicae) (no pattern category).

Types Ia_1, Ib, IIIa, $IIIa_1$, IV, V, VIb and VIc are the major types of strobilar organization of two, three, four, seven, and nine species in various groups (Table 4).

As may be gleaned from Table 5, (1) nine species exhibit only one type of strobilar organization. These are: *S. tamariscina* (Type Ic), *S. copelandii* (Type VIb), *S elmeri* (Type IVb), *S. uncinata* (Type IIIa; Dahlen 1982, 1988), *S. atimonanensis* (Type Ia_1; Tan and Jermy 1981), *S. ciliaris* (Type V), *S. pricei* (Type IV; Tan and Jermy 1981), *S. heterostachys* (Type IIIa; Dahlen 1982, 1988), *S. willdenovii* (Type IV); (2) 32 species exhibit more than one type of strobilar organization (ranging from 2–5 types) with *S. involvens* displaying the most number of five types (Types Ib, IV, V, VIa and VIc). The occurrence of both Types IV and V in the same species is interesting (see possible significance below).

Some interesting variations in strobilar morphology. Some uncommon variations in strobilar morphology were noted during the course of the studies. These include: (1) production of forked strobili (*S. negrosensis, S. cupressina*), (2) production of axillary strobili (*S. jagorii*), (3) occurrence of the 'growing through' phenomenon (*S. tamariscina, S. involvens, S. cupressina, S. delicatula, S. aristata*), (4) complete non-development of the sporangia at the upper side (median plane) of the strobili resulting in the presence of only two rows of mature megasporangia (*S. llanosii*), and (5) production of many strobili with only mature megasporangia and a few small non-developed sporangia scattered here and there throughout the length of the strobili, a condition which is referred to here as functionally megasporophyllic, yet in actual count, it can be reckoned under Type V. The foregoing variations have earlier been reported by other workers in other species (Goebel 1905; Mitchell 1910; Duerden 1929; Graustein 1930; Tryon, 1955; Horner and Arnott 1963; Zamora 1971; De la Sota and Morbelli 1981).

Trends in evolution of the Selaginella *strobilus.* Of the 12 types and subtypes of strobilar organization based on the arrangement of sporophylls here recognized, Type Ia (strobili with a basal zone of megasporophylls + an apical zone of microsporophylls) is chosen as the basic type from which could have arisen the most specialized derived types, viz., Type IV (strobili which consist wholly or predominantly of microsporophylls) and Type V (strobili which consist wholly or predominantly of megasporophylls) for the following reasons: (1) Type Ia is presumed to be the basic type because it characterized many fossil members of the family Selaginellaceae, i.e., *Selaginellites* (Hoskins and Abbott 1956; Foster and Gifford 1959; Leisman 1961). This type contains

both types of sporophylls (megasporophylls, microsporophylls); (2) Types IV and V are presumed the most specialized derived types among the various types or subtypes in that these two types contain only one kind of sporophylls (either megasporophylls or microsporophylls) (Goebel 1905; Bower 1908; Horner and Arnott 1963); and (3) The various other types or subtypes are presumed to represent the intermediate stages in the process of derivation leading to the formation of the most specialized types because they can be located somewhere between the basic type and the most specialized derived types.

Essentially, the pathway here proposed is similar to that of Horner and Arnott (1963) with minor modifications in the light of the data presented by Jermy et al. (1967), Pettitt (1970, 1971), Tryon (1971), and the present workers. Indicated in Figure 3 are the major types of strobilar organization together with the respective species possessing them.

In discussing relationships between the basic type and the most specialized derived types, the latter are presumed to have been derived from the former via the discontinuance or continuance of the sporophyll development processes (megasporophyllization, microsporophyllization) influenced by a complex interplay of environmental and genetical factors which remain to be investigated.

If the set of factors favors megasporophyllization, the result is Type V pattern of strobilar organization. If, however, the said set of factors favors microsporophyllization, the result is Type IV pattern. The processes of megasporophyllization or microsporophyllization may become arrested at any time vis-a-vis the operationalization of the set of factors. The arrest of development results in the functionally microsporophyllic type (Type IV? in the diagram) or the functionally microsporophyllic type (Type V? in the diagram) as the case may be (Figure 4). Morphologically, the functionally megasporophyllic type consists of a mixture of mature megasporophylls + non-developed sporophylls among the mature ones, while the functionally microsporophyllic type consists of a mixture of mature microsporophylls + non-developed sporophylls. The presence of the non-developed sporophylls among the mature ones is taken as evidence of the arrest of development of said structures. In further support of the foregoing is the set of data presented in Table 6 on the occurrence in four species (belonging to different groups from various geographical sources) of both Type IV (strobili with wholly microsporophyllic strobilar pattern) and Type V (strobili with wholly megasporophyllic strobilar pattern).

There seems to be several pathways by which the most specialized derived types of strobilar organization (Type IV and Type V) can arise from the presumed basic type (Type Ia), thus: (1) via Type Ia, (2) via Type Ic, (3) via Types IIIa–IIIa$_1$, and (4) via Types IIIa-Ia$_1$. These are represented diagrammatically in Figures 3 and 4 which are self-explanatory.

SUMMARY

Based on the analyses of more than 2,000 cleared strobili of 37 Philippine species of *Selaginella* + a consideration of data on four species from published sources, six types and six subtypes of strobilar organization are recognized. These are: Type I (strobili with a basal zone of megasporophylls and an apical zone of microsporophylls or a mixture of both kinds of sporophylls (with three subtypes), Type II (strobili with two median rows of microsporophylls and two lateral rows of megasporophylls), Type III (strobili with two median rows of microsporophylls and two lateral rows of basal megasporophylls with an upper portion of microsporophylls or a mixture of megasporophylls and microsporophylls (with one subtype), Type IV (strobili made up wholly or overwhelmingly of microsporophylls), Type V (strobili made up wholly or overwhelmingly of megasporophylls), and Type VI (strobili with a basal zone of microsporophylls and an apical zone of microsporophylls and megasporophylls (with two subtypes).

Nine species exhibit only one type of strobilar organization. These are: (1) *S. tamariscina* (Type Ic), (2) *S. copelandii* (Type VIb), (3) *S. elmeri* (Type VIb), (4) *S. uncinata* (Type IIIa, Dahlen 1982, 1988), (5) *S. atimonanensis* (Type Ia$_1$, Tan and Jermy 1981), (6) *S. ciliaris* (Type V), (7) *S. pricei* (Type IV, Tan and Jermy 1981), (8) *S. heterostachys* (Type IIIa, Dahlen 1982, 1988) and (9) *S. willdenovii* (Type IV). Thirty-two species exhibit more than one type of strobilar organization (ranging from 2–5 types) with *S. involvens* displaying the highest number of five types (Types Ib, IV, V, VIa and VIc).

Most of the species that make up the groups in the two sections and subsections in the subgenus Heterophyllum vis-a-vis v A v R's system of classification show similar types of strobilar organization; said similarities are taken as indication of the taxonomic value of the character at the level of the group and section (but not at the level of the species). As a character, strobilar organization may also point out probable discrepancies in taxonomic placement of certain taxa.

Some noteworthy variations in strobilar morphology are reported. These include: (1) forking strobili, (2) 'growing through' phenomenon, (3)

axillary strobili, (4) complete non-development of sporangia at the median plane of strobili resulting in only two rows of megasporophylls and others.

In evolutionary terms, Type Ia is considered the basic type of strobilar organization from which Type IV and Type V (the most specialized derived types) could have been derived as evidenced from (1) the occurrence of Types Ia_1, II, IIIa, $IIIa_1$, VIa, VIb, VIc (the intermediate types) and (2) the occurrence of both Type IV and Type V in the same species.

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Table 1. Forty-one Philippine species of *Selaginella* covered in this paper vis-a-vis v A v R's system of classification

Subgenus Heterophyllum
- Section Monostelicae
  - Subsection Homeostachys
    - Group Rosulantes (*S. tamariscina*)
    - Group Decumbentes (No local representative)
    - Group Radicantes (*S. auriculata,* S. negrosensis,* S. remotifolia*)
    - Group Ascendentes (*E. agusanensis,* S. alligans, S. copelandii,* S. cumingiana,* S. elmeri,* S. fenixii,* S. jagorii* (*S. halconensis*),* *S. intermedia* (*S. ascendens*), *S. magnifica, S. repanda*)
    - Group Caulescentes (*S. cupressina, S. involvens* (*S. polyura, S. peltata*), *S. luzonensis,* S. moellendorffii)*
    - Group Pubescentes (*S. flagellifera* (*S. biformis*), *S. uncinata*)
  - Subsection Heterostachys
    - Group Intertexta (*S. atimonanensis,* S. ciliaris, S. intertexta,* S. nummularia, S. pricei**)
    - Group Bisulcatae (*S. boninensis, S. opaca*)
    - Group Proniflorae (*S. heterostachys*)
    - Group Suberosae (*S. aristata, S. eschscholzii,* S. llanosii, S. myosuroides,* S. philippina**)
    - Group Brachystachyae (*S. ornata*)
- Section Pleiostelicae (*S. delicatula, S. gastrophylla, S. lacerata,* S. plana, S. englerii,* S. usterii, S. wildenovii*)

The following nine species have not become available for study: *S. longiaristata (S. springiana)* (Group Radicantes), *S. aenea,* S. latifrons,* S. heelii,* S. presliana,* S. procera, and *S. ramosii** (Group Ascendantes), *S. flabelloides** (Group Caulescentes), *S. apoensis* (Goup Intertexta).**

***Endemic**

Table 2. Descriptions of the types and subtypes of strobilar organization in 41 Philippine species of *Selaginella*

Types	Descriptions
Ia	Strobili with a basal zone of megasporophylls and an apical zone of microsporophylls.
Ia_1	Strobili with a large basal megasporophyll + the rest of the axis with microsporophylls.
Ib	Strobili with a basal zone of megasporophylls and an apical zone with randomly arranged microsporophylls and megasporophylls.
Ic	Strobili with a basal zone of megasporophylls and an apical zone of two median (dorsal) rows of microsporophylls and two lateral (ventral) rows of megasporophylls.
II	Strobili with two median (dorsal) rows of microsporophylls + two lateral (ventral) rows of megasporophylls.
III_a	Strobili with two median (dorsal) rows of microsporophylls + two lateral (ventral) rows of megasporophylls at the base and an apical zone of microsporophylls.
$IIIa_1$	Strobili with two median (dorsal) rows of microsporophylls + two lateral (ventral) rows of basal portion with megasporophylls and apical portion of mixture of microsporophylls and megasporophylls.
IV	Strobili which consist wholly (or predominantly) of microsporophylls.
V	Strobili which consist wholly (or predominantly) of megasporophylls.
VI_a	Strobili with a basal zone of microsporophylls + an apical zone of megasporophylls and microsporophylls interspersed with non-developed sporophylls.
VI_b	Strobili with a basal zone of microsporophylls + an apical zone of two median (dorsal) rows of microsporophylls and two lateral (ventral) rows of megasporophylls.
VI_c	Strobili with a basal zone of microsporophylls and an apical zone of two median (dorsal) rows of microsporophylls and two lateral (ventral) rows of mixed sporophylls.

Table 3. Number of strobili examined and the percentage of strobili exhibiting the types and subtypes of strobilar organization in 41 Philippine species of *Selaginella*

	Species	No. of Strobili Examined	Percentage of Strobili Exhibiting Types & Subtypes											
			Ia	Ia_1	Ib	Ic	II	IIa	IIa_1	IV	V	VIa	VIb	VIc
1.	*S. tamariscina*	24	–	–	–	100	–	–	–	–	–	–	–	–
2.	*S. auriculata*	10	–	–	–	–	–	–	20	–	–	–	–	80
3.	*S. negrosensis*	73	–	–	–	–	48	12	–	–	29	–	–	11
4.	*S. remotifolia*	30	33	67	–	–	–	–	–	–	–	–	–	–
5.	*S. agusanensis*	10	–	–	–	–	–	–	–	10	–	–	60	30
6.	*S. alligans*	20	–	–	–	–	–	–	–	–	–	–	85	–
7.	*S. copelandii*	10	–	–	–	–	–	–	–	–	–	–	100	–
8.	*S. cumingiana*	23	–	–	–	–	–	–	–	13	–	–	87	–
9.	*S. elmeri*	10	–	–	–	–	–	–	–	–	–	–	100	–
10.	*S. fenixii*	20	–	–	–	–	–	–	–	–	–	–10	10	80
11.	*S. intermedia*	10	–	–	–	–	–	70	–	–	–	–	10	20
12.	*S. jagorii*	70	–	–	–	–	–	–	–	2	–	–	64	34
13.	*S. magnifica*	30	–	–	–	–	–	–	–	–	–	–	17	83
14.	*S. repanda*	36	11	–	–	–	–	–	–	–	89	–	–	–
15.	*S. cupressina*	51	–	–	–	–	6	–	–	19	–	–	20	55
16.	*S. involvens*	143	–	–	46	–	–	–	–	17	28	2	–	7
17.	*S. luzonensis*	16	–	–	–	–	–	–	–	12	–	–	88	–
18.	*S. moellendorffii*	38	–	–	–	–	5	–	–	–	–	–	21	74
19.	*S. flagellifera*	41	–	–	–	–	–	14	–	20	–	–	–	66
20.	*S. unchata*	–	–	–	–	–	–	a	–	–	–	–	–	–

21.	*S. atimonanensis*	–	–	b	–	–	–	–	–	–	–	–	–	–
22.	*S. ciliaris*	30	–	–	–	–	–	–	–	–	100	–	–	–
23.	*S. intertexta*	57	2	–	–	–	4	–	58	–	36	–	–	–
24.	*S. nummularia*	46	–	–	–	–	–	20	–	26	54	–	–	–
25.	*S. pricei*	–	–	–	–	–	–	–	–	c	–	–	–	–
26.	*S. boninensis*	40	–	–	–	–	–	17	–	–	83	–	–	–
27.	*S. opaca*	25	12	20	68	–	–	–	–	–	–	–	–	–
28.	*S. heterostachys*	–	–	–	–	–	–	d	–	–	–	–	–	–
29.	*S. aristata*	51	–	–	–	–	–	–	–	20	80	–	–	–
30.	*S. eschscholzii*	38	–	79	–	–	–	–	–	21	–	–	–	–
31.	*S. lianosi*	36	5	–	–	–	–	–	–	–	95	–	–	–
32.	*S. myosuroides*	65	–	–	–	–	3	66	–	31	–	–	–	–
33.	*S. philippina*	98	5	–	–	–	–	–	–	10	85	–	–	–
34.	*S. ornata*	31	–	–	–	–	13	87	–	–	–	–	–	–
35.	*S. delicatula*	62	–	–	–	–	–	–	–	37	–	–	–	63
36.	*S. gastrophylla*	20	–	–	–	–	–	–	–	80	–	20	–	–
37.	*S. lacerata*	16	–	–	–	–	–	–	–	12	–	63	–	25
38.	*S. plana*	40	–	–	–	–	–	–	–	–	–	–	–	–
39.	*S. engleri*	30	–	–	–	–	–	–	–	33	–	–	–	67
40.	*S. usterii*	25	–	–	–	–	–	–	–	40	–	–	–	60
41.	*S. wildenovii*	60	–	–	–	–	–	–	–	100	–	–	–	–

Data consolidated from Zamora (1971), Balagat (1971), Bagaoisan-Cosico (1972), Tan (1974) and Mercado (1990).

Species 1 (Group Rosulantes), Species 2–4 (Group Radicantes), Species 5–4 (Group Ascendentes), Species 15–18 (Group Caulescentes), Species 19–20 (Group Pubescentes), Species 21–25 (Group Intertexta), Species 26–27 (Group Bisulcatae), Species 28 (Group Proniflorae), Species 29–33 (Group Suberosae), Species 34 (Group Brachystachyae) Species 35–41 (Section Pleiostelicae).

a, reported by Dahlen (1982).

b, reported by Tan and Jermy (1981).

c, reported by Tan and Jermy (1981). d, reported by Dahlen (1982).

Species 11 (*S. ascendens* is a synonym of *S. intermedia*). Species 12 (*S. halconensis* is a synonym of *S. jagorii*). Species 16 (*S. polyura* and *S. peltata* are synonyms of *S. involvens*). Species 19 (*S. bifurmis* is a synonym of *S. flagelliflora*).

Table 4. Forty-one Philippine species of *Selaginella* and the major types of strobilar organization that characterize them.

Types	Species and Their Respective Groups	No.of Species
Ia		0
Ia_1	*S. remotifolia* (Group Radicantes), *S. eschscholzii* (Group Suberosae), *S. atimonanensis* (Group Intertexta)	3
Ib	*S. involvens* (Group Caulescentes), *S. opaca* (Group Bisulcatae)	2
Ic	*S. tamariscina* (Group Rosulantes)	1
II	*S. negrosensis* (Group Radicantes)	1
IIIa	*S. intermedia* (Group Ascendentes), *S. myosuroides* (Group Suberosae), *S. heterostachys* (Group Proniflorae), *S. ornata* (Group Brachystachyae)	4
$IIIa_1$	*S. uncinata* (Group Pubescentes), *S. intertexta* (Group Intertexta)	2
IV	*S. pricei* (Group Intertexta), *S. gastrophylla* and *S. willdenovii* (Section Pleiostelicae)	3
V	*S. repanda* (Group Ascendentes), *S. ciliaris* and *S. nummularia* (Group Intertexta), *S. boninensis* (Group Bisulcatae), *S. aristata*, *S. llanosii* and *S. philippina* (Group Suberosae)	7
VIa	*S. lacerata* (Section Pleiostelicae)	1
VIb	*S. agusanensis*, *A. alligans*, *S. copelandii*, *S. cumingiana*, *S. elmeri* and *S. jagorii* (Group Ascendentes), *S. luzonensis* (Group Caules centes)	7
VIc	*S. auriculata* (Group Radicantes), *S. fenixii* and *S. magnifica* (Group Ascendentes). *S. cupressina* and *S. moellendorffii* (Group Caulescentes), *S. flagellifera* (Group Pubescentes), *S. delicatula*, *S. engleri* and *S. usterii* (Section Pleiostelicae)	9
No Pattern	*S. plana* (Section Pleiostelicae)	1
TOTAL		41

Table 5. Number of types and subtypes of strobilar organization in 41 Philippine species of *Selaginella*

	Species	No. of Types		Species	No. of Types
1.	*S. tamariscina*	1	21.	*S. atimonanensis*	1
2.	*S. auriculata*	2	22.	*S. ciliaris*	1
3.	*S. negrosensis*	4	23.	*S. intertexta*	4
4.	*S. remotifolia*	2	24.	*S. nummularia*	3
5.	*S. agusanensis*	3	25.	*S. pricei*	1
6.	*S. alligans*	2	26.	*S. boninensis*	2
7.	*S. copelandii*	1	27.	*S. opaca*	3
8.	*S. cumingiana*	2	28.	*S. heterostachys*	1
9.	*S. elmeri*	1	29.	*S. aristata*	2
10.	*S. fenixii*	3	30.	*S. eschscholzii*	2
11.	*S. intermedia*	3	31.	*S. llanosii*	2
12.	*S. jagorii*	3	32.	*S. myosuroides*	3
13.	*S. magnifica*	2	33.	*S. philippina*	3
14.	*S. repanda*	2	34.	*S. ornata*	2
15.	*S. cupressina*	4	35.	*S. delicatula*	2
16.	*S. involvens*	5	36.	*S. gastrophylla*	2
17.	*S. luzonensis*	2	37.	*S. lacerata*	3
18.	*S. moellendorffii*	3	38.	*S. plana*	0
19.	*S. flagellifera*	3	39.	*S. englerii*	2
20.	*S. uncinata*	1	40.	*S. usteri*	2
			41.	S. wildenovii	1

Table 6. Occurrence of both type IV and V of strobilar organization in the same Philippine species of *Selaginella*.

	Species	No. of Strobili Examined	Percentage of Strobili Exhibiting Types						
			IV	V	Ia	Ib	IIIa	VIa	VIc
16	*S. involvens*[a]	143	17	28	–	46	–	2	7
24	*S. nummularia*[b]	46	26	54	–	–	20	–	–
29	*S. aristata*[c]	51	20	80	–	–	–	–	–
33	*S. philippina*[c]	98	10	85	5	–	–	–	–

[a]Group Caulescentes, [b]Group Intertexta, [c]Group Suberosae

Source of materials. *S. involvens:* Type IV (17%) Mt. Banahao (Luzon). Type V (28%) Mindoro, Bukidnon (Mindanao). Type Ib (46%) Pampanga, Rizal and Laguna (Luzon), Mindoro, Negros (Visayas), Taiwan. Type VIa (2%) Benguet, Bataan (Luzon), Taiwan. Type Ic (7%) Benguet, Pampanga and Mt. Makiling (Luzon).

S. nummularia: Type IV (26%) Mt. Makiling (Luzon). Type V (54% Mt. Makiling (Luzon), Negros (Visayas). Type IIIa (20%) Mt. Makiling (Luzon), Cebu (Visayas).

S. aristata: Type IV (20%) Benguet (Luzon). Type V (80%) Mt. Makiling (Luzon). Samar (Visayas).

S. philippina: Type IV (10%) Benguet (Luzon). Type V (85%) Benguet, Mt. Makiling (Luzon). Type Ia (5%) Mt. Makiling (Luzon).

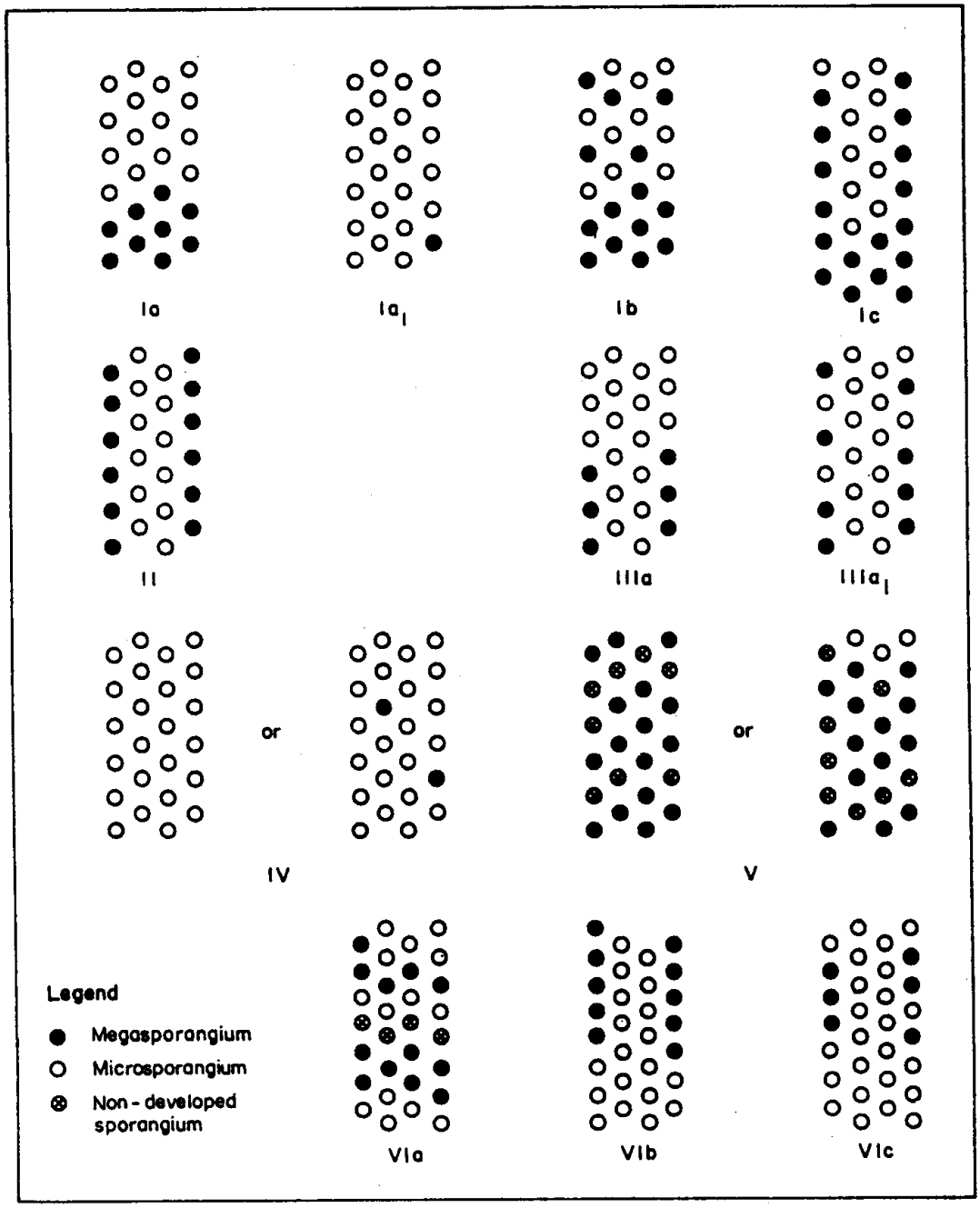

Fig.1. Diagrammatic representation of the different types and subtypes of strobilar organization described in Philippine species of *Selaginella*.

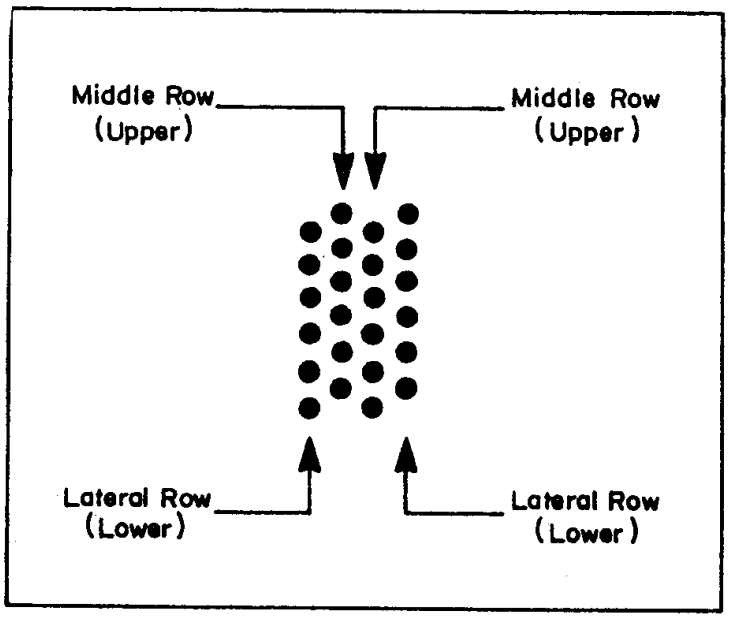

Fig. 2. Diagram depicting the distribution of sporophylls along the strobilar axis in *Selaginella*.

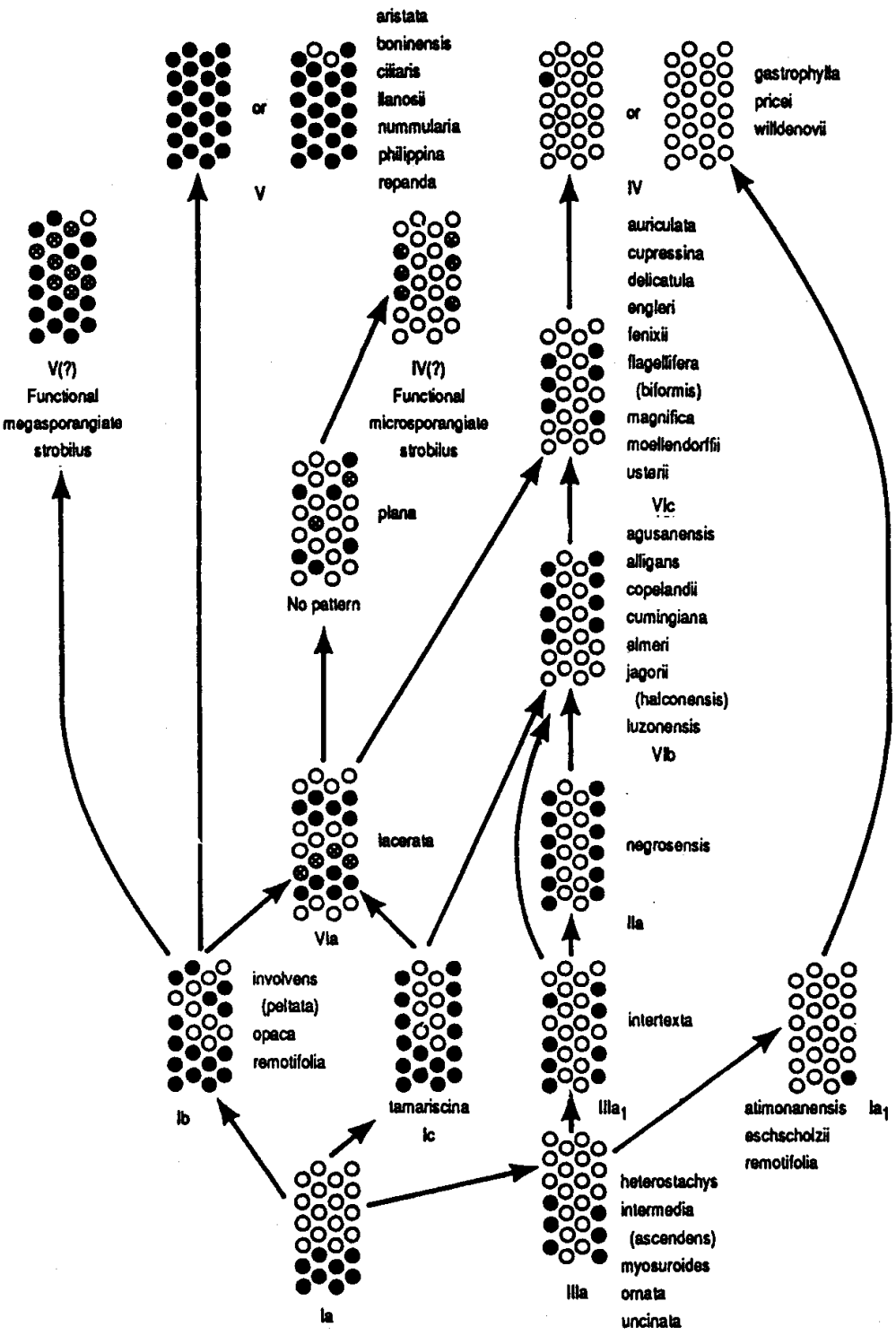

Fig. 3. Summary of major types and subtypes of strobilar organization exhibited by Philippine species of *Selaginella*. Arrows indicate possible lines of phyletic development. Solid circles represent megasporangia, open circles represent microsporangia and crossed circles represent non-developed sporangia.

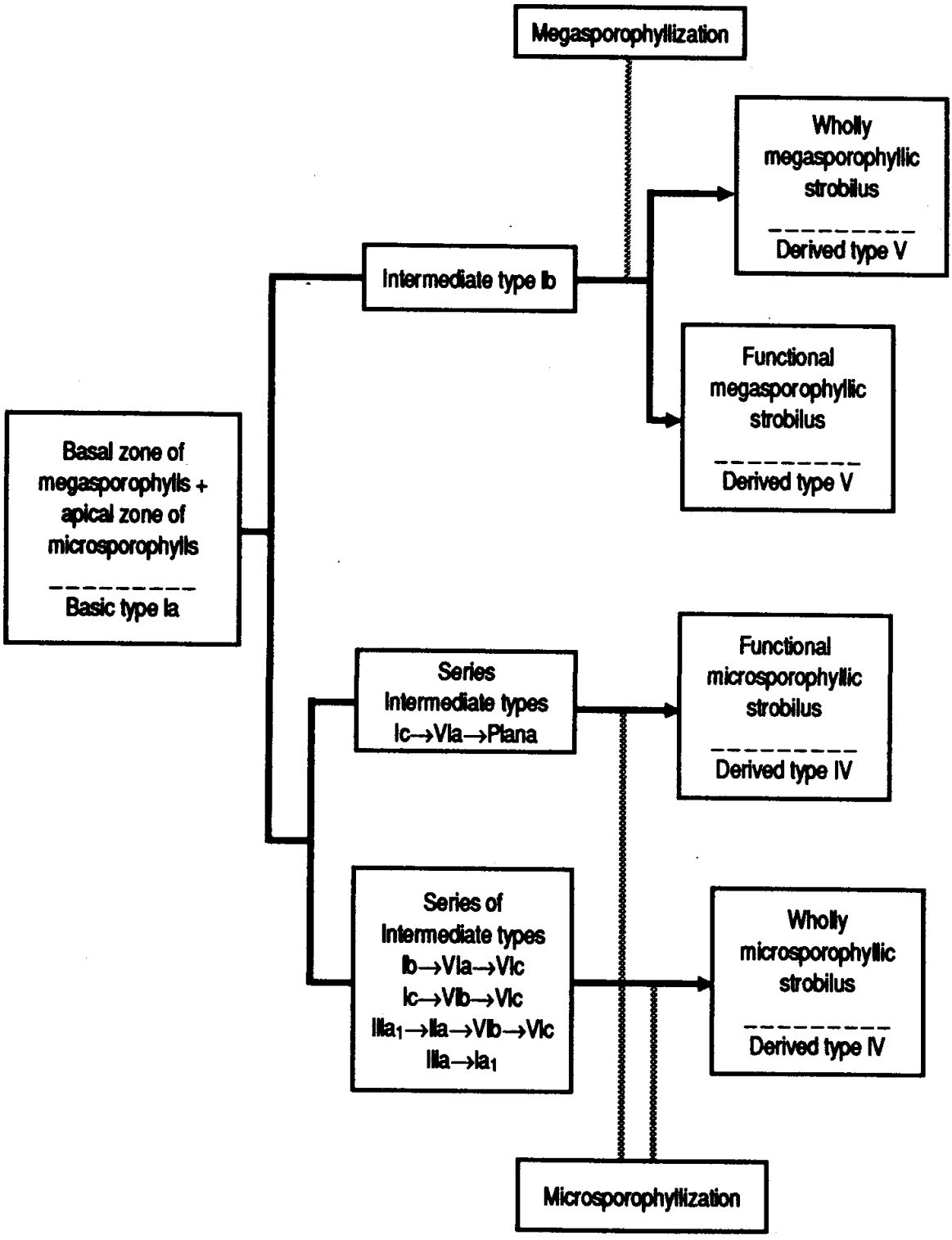

Fig. 4. Schematic representation of the suggested pathways in the possible derivation of the megasporophyllic condition and the microsporophyllic condition from the presumed basic strobilic condition (one with a basal zone of megasporophylls and an apical zone of microsporophylls).