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A HETEROSPOROUS SPECIES OF BOWMANITES FROM THE MICHIGAN COAL BASIN [1]

Chester A. Arnold

THE VARIOUS members of the Sphenopsida, both living and fossil, are generally regarded as essentially homosporous, although it cannot be said that heterospory is nonexistent within the group. In *Equisetum* the spores produced by a single plant are alike in size, but they grow into gametophytes some of which bear only antheridia and others only archegonia. The gametophytes are therefore dioecious even though true heterospory is not revealed. In the fossil genus *Calamites* a slight difference in spore size of some species has long been looked upon as an indication of incipient heterospory, even though the two kinds of spores may occur within identical sporangia on the same sporangiophore. Other species of *Calamites* are believed to be strictly homosporous. In *Sphenophyllum* homospory is believed by most authors to have prevailed although heterospory has been reported in a few instances. Renault (1876) described and figured what he thought was a megaspore within the sporangium of a fructification assigned to *Sphenophyllum Dawsoni,* but the object was evidently a misplaced fragment of the sporangial wall. Several years later Thoday (1906) observed a difference in spore size within a sporangium attributed to the same species. In one sporangium the spores ranged up to 120 micra in diameter but averaged 106 micra, and in the adjacent sporangium the average size was 83 micra. Zobel (1910) figured what he supposed were the microsporangia and megasporangia of *S. verticillatum,* but as he found spores only within the former, heterospory, though suggested, was not demonstrated. Lacking indisputable evidence, therefore, of heterospory in *Sphenophyllum,* most authors have concluded that homospory must have been the rule throughout this group of plants (Scott, 1920; Walton, 1940; Hoskins and Cross, 1943). Hoskins and Cross include homospory as a generic character in their revised diagnosis of the organ genus *Bowmanites* to which they refer all fructifications attributable to *Sphenophyllum.* A few authors, on the other hand, make some allowances. Hirmer (1927) cites *S. verticillatum* as an isolated example of heterospory within the genus, and Eames (1936) says that although most species are homosporous, a few are known to have been heterosporous. Although Eames cites no examples, his generalization is now known to be correct.

The present account is concerned with a sphenophyllaceous fructification which is distinctly heterosporous. Not only is the phenomenon clearly demonstrable, but it is as pronounced, as far as difference in spore size is concerned, as in the recent lycopod *Selaginella.* This instance merely shows that in the Sphenopsida, and within *Sphenophyllum* in particular, both homospory and well-defined heterospory existed. Differences in spore size may not

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necessarily be correlated with any observable differences in the size of the sporangia, and there is no evidence whatsoever in our material of segregation in different parts of the strobili.

SOURCE.—The fructifications described in this account came from a shale bed below the "lower *Lingula* layer" in the quarry of the Grand Ledge Clay Products Company, at Grand Ledge, Michigan. This shale lies just below Cycle "A" of the Pre-Verne cyclical formations of the Saginaw group as outlined by Kelly (1936) and is of Pottsville (early Pennsylvanian) age. This horizon has yielded a flora of considerable size.

DESCRIPTION.—The material consists of fragments of a number of individual strobili preserved as carbonized compressions (fig. 1, 2). None of the strobili are complete, and none are attached to the vegetative parts. This detached and fragmentary condition suggests that the organs were transported for some distance before they sank into the muddy bottom. In a few specimens believed to belong to this species the whorls of coalescent sterile bracts are partially preserved, but preservation is inadequate to reveal the exact relation of the sterile bracts and the sporangiophores. On most of the specimens, only the sporangia are preserved, and inferences concerning the morphology and affinities are drawn mostly from the gross aspect and the arrangement of the sporangia.

The strobili are approximately 1.70 cm. broad and at least 10 cm. long, although none were found complete. It is unlikely, however, that any of them were originally much longer. The sides are parallel for most of the length and the bases and apices are rather abruptly rounded. The sporangia are arranged in verticels spaced at intervals of about 5 mm. The sporangiophores are not preserved, but it is evident from the packed condition and the large number of sporangia per whorl that the stalks were of different lengths, with shorter ones bearing sporangia near the axis and longer ones bearing others at the outer circumference of the verticel. There are many sporangia per verticel; although the number can only be crudely estimated, there are at least sixty and maybe more. In those specimens with well preserved sporangia nothing remains of the intervening whorls of bracts which subtended the sporangiophores.

The sporangia are ovoid bodies measuring 1.75 by 2.50 mm., and appear to be borne in pairs on the upturned distal ends of the sporangiophores. In many of the specimens the individual sporangia can be lifted as tissue-thin bodies with the point of a knife blade or a dissecting needle. Several of these were placed singly in test tubes and treated with Schulze's reagent (potassium chlorate and concentrated nitric acid). The maceration process removed the dark coloring matter and revealed the spore contents, and in this way it was possible to determine the kind of spores present in each one. Due to the fact that the carbonized material of the fructifications consists almost wholly of the compressed sporangia, and since these could be removed from their original position free from extraneous matter, there is no alternative but that the two kinds of spores observed belong to the same fructification. The verticillate arrangement and the packed condition of the sporangia are shown in figures 1 and 2. This specimen is incomplete and lacks both the apex and base, but it is selected as the type because of the clarity with which the sporangia are shown.

The sphenophyllaceous affinities of the fructification are obvious from the size, number, and arrangement of the sporangia within the verticels. In fact, in no sphenopsid fructifications except those assigned to *Sphenophyllum* are the sporangia ever arranged in concentric circles within the verticels. This arrangement is due to the fact that each sterile bract bears more than one axillary sporangiophore (although some species possess but one) and they are of unequal length, well known examples being *Bowmanites Dawsoni, B. Römeri* and *B. trisporangiatus,* the latter recently described by Hoskins and Cross (1943). There is no evidence whatsoever in our material of the peltate type of sporangiophore found in *Calamites* and *Equisetum.*

Upon prolonged maceration the sporangial wall dissolves away and the masses of cutinized spores contained within are freed. Most of the sporangia contain a large number of very small round smooth-walled spores which range from 75 to 90 micra in diameter (fig. 3, 5). Figure 3 shows the contents of a single microsporangium enlarged twenty-five times. The spores are very loosely held together, and unless carefully handled the mass disintegrates. Many of them still adhere in tetrads (fig. 9). It should be noted that these microspores agree closely with the dimensions usually given for those *Sphenophyllum* spores which are usually regarded as isospores. Hoskins and Cross (1943), who have brought together practically all of the published data on spore size in the fructifications of *Sphenophyllum* give the following dimensions:

Bowmanites Scottii—65–85 micra including perispore
B. Dawsoni—75–100 micra including perispore
B. trisporangiatus—100–150 micra including perispore
75–125 micra without perispore
B. Römeri—100 micra
B. fertilis—90–96 × 65–70 micra without perispore

The perispore is not included in the dimensions given for our material and the existence of this layer is problematic, but it seems significant to note that the dimensions (75–90 micra) are about the average for those given for the genus as a whole.

A few of the sporangia, probably one among every eight or ten present in the carbonized strobili, contain large spherical or slightly ovoid spores which range in size from 580 × 665 micra to 750 × 750 micra. Figure 6 shows the contents of such a sporangium enlarged twenty-five times (the same as fig. 3 which shows the microspores). These large

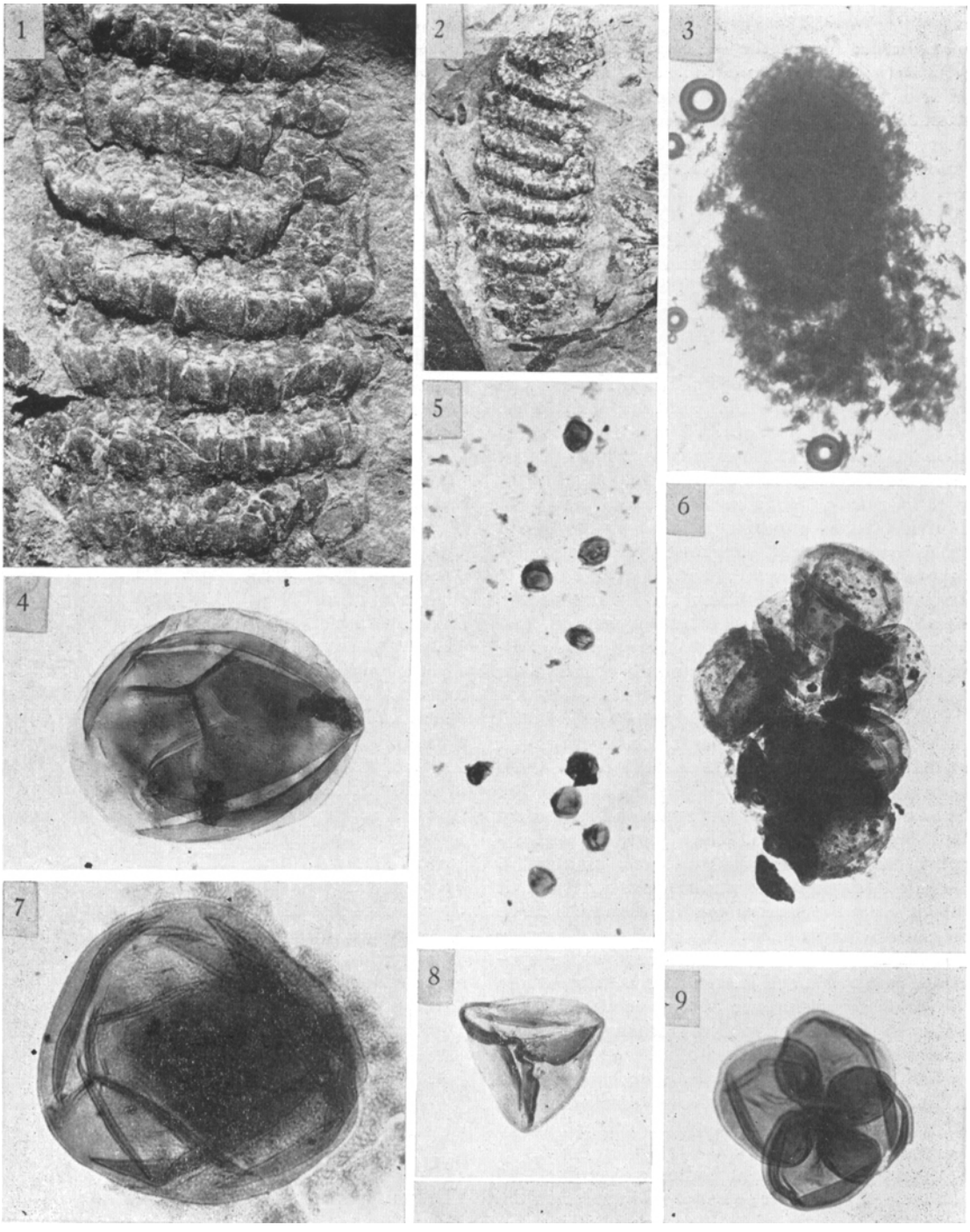

Fig. 1–9.—Fig. 1. Enlarged view of holotype specimen showing the closely packed, verticillately arranged, oval sporangia. × 2.9.—Fig. 2. Specimen shown in figure 1. Natural size.—Fig. 3. Contents of a single microsporangium freed by maceration. × 25.—Fig. 4. Single megaspore showing tetrad scar. × 64.—Fig. 5. Isolated microspores. × 64.—Fig. 6. Contents of a single megasporangium showing the fully formed and aborted megaspores. × 25.—Fig. 7. Single megaspore. × 64.—Fig. 8. Aborted megaspore. × 64.—Fig. 9. Microspore tetrad. × 240.

spores, the megaspores (fig. 4, 7), have thin smooth walls, and show a conspicuous tetrad scar. About sixteen of these megaspores appear to be present within a sporangium although the exact number is uncertain. Not all of the megaspores reached maturity. Within the mass, among the fully formed spores, there are a few aborted members which are about one-third as large as the fully formed ones

(fig. 8). At least two aborted megaspores may be seen in figure 6. One lies at the bottom of the figure slightly detached from the mass, and another appears as a triangular opaque area near the upper right side. Not all of these aborted spores are triangular. Many are rounded like the mature ones, but their walls are always slightly darker and less readily bleached during the maceration process. Each megaspore is probably surrounded by a perispore, but little or nothing has been determined concerning the character of this layer. Its presence is suggested in some instances by fragments of disorganized material around the exine.

It is evident that as far as spore size is concerned, heterospory is as well developed in this form as in many of the ancient and modern lycopods (*Lepidodendron, Selaginella,* etc.). There is, however, no discernible difference in the external appearance of the sporangia bearing the two types, nor is there any apparent segregation in different parts of the cones. The megaspores and microspores are borne in sporangia alike in size and shape, and in the same verticels.

Although the structure of large organs cannot be worked out with the same degree of exactitude by maceration of carbonized remains as with thin sections of petrifactions, the maceration method is not without distinct advantages. It enables one to examine a much wider range of materials than is usually possible with sections, and in addition such objects as spores can be observed in their entirety and large quantities measured. This is rather difficult in thin sections. Maceration, of course, requires care on the part of the investigator to eliminate extraneous material, but in a situation such as that under consideration here, the different parts can be handled individually, so there is no cause to question the validity of the results obtained. If only a few large spores were to be observed among a multitude of smaller ones, their presence could be explained as accidental, but when they occur in abundance and can be observed *in situ* within the original sporangia which were individually removed from the fructification, they may be accepted as proof of a true heterosporous condition.

Taxonomy.—The fructification described here is referred to the organ genus *Bowmanites* (Binney, 1870). This name, according to Hoskins and Cross (1943) is the correct one for detached sphenophyllaceous strobili, as it has priority over *Sphenophyllostachys* which was proposed by Seward (1898). *Volkmannia,* a name of still older standing, was founded upon organs now known to belong to *Calamites.* However, in assigning this material to *Bowmanites,* it is necessary to broaden the concept of the genus as given by Hoskins and Cross so as to admit heterosporous forms. The only other alternative is to create for our material a new genus which is considered inadvisable for at least two reasons. In the first place, our form is not sufficiently preserved to serve as a generic type, and secondly, homospory is not such a constant feature among the sphenophylls as Hoskins and Cross have assumed. It has already been pointed out that the microspores in our form are similar in size to the alleged isospores of some of the other species. At present it is impossible to divide *Bowmanites* on the basis of spore condition, because in no other species have spores been reported that in any way approach the megaspores of our form in size. It is quite probable that such types as *Bowmanites Scottii* and *B. fertilis* might be found to be heterosporous were the spore condition in these fully known, and the same might be predicted for *B. Römeri* which apparently is known from a very limited amount of material. The generic diagnosis of *Bowmanites* should be broad enough to include both homosporous and heterosporous forms.

Bowmanites **delectus** sp. nov.—Strobili large, about 1.70 cm. in diameter and at least 10 cm. long, linear; sporangia ovoid, 1.75 × 2.50 mm., borne in pairs and in whorls spaced at intervals of 5 mm. on the axis, numerous (60 or more per whorl) and closely packed; heterosporous; megasporangia and microsporangia similar except for spore content and produced in the same whorls; microspores numerous, 75–90 micra in diameter, smooth; megaspores spherical or slightly ovoid, thin walled, smooth, 660–750 micra in greatest diameter, about 16 in each sporangium; a few aborted megaspores having about one-third the diameter of the mature ones; perispore probably present; tetrad scar conspicuous in both types. Holotype No. 23415 University of Michigan Collection.

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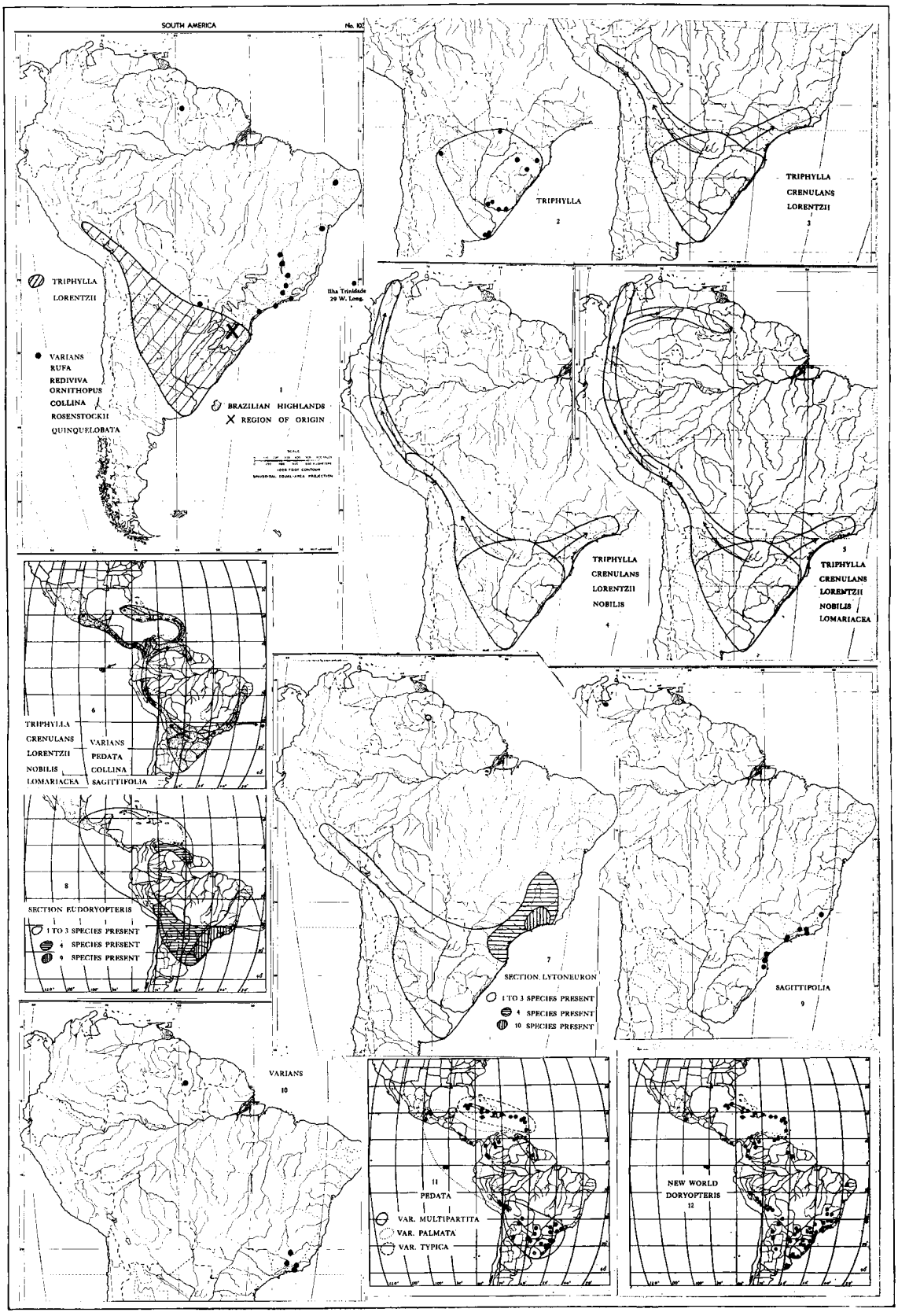
SOUTH AMERICA
TRIPHYLLA
LORENTZII
VARIANS
RUFA
REDIVIVA
ORNITHOPUS
COLLINA
ROSENSTOCKII
QUINQUELOBATA
BRAZILIAN HIGHLANDS
REGION OF ORIGIN
Ilha Trindade
29 W. Long.
1
TRIPHYLLA
2
TRIPHYLLA
CRENULANS
LORENTZII
3
TRIPHYLLA
CRENULANS
LORENTZII
NOBILIS
4
5
TRIPHYLLA
CRENULANS
LORENTZII
NOBILIS
LOMARIACEA
6
TRIPHYLLA
CRENULANS
LORENTZII
NOBILIS
LOMARIACEA
VARIANS
PEDATA
COLLINA
SAGITTIPOLIA
8
SECTION EUDORYOPTERIS
1 TO 3 SPECIES PRESENT
4 SPECIES PRESENT
9 SPECIES PRESENT
7
SECTION LYTONEURON
1 TO 3 SPECIES PRESENT
4 SPECIES PRESENT
10 SPECIES PRESENT
SAGITTIPOLIA
9
VARIANS
10
11
PEDATA
VAR. MULTIPARTITA
VAR. PALMATA
VAR. TYPICA
NEW WORLD
DORYOPTERIS
12