INVESTIGATIONS OF NORTH AMERICAN CYCADEOIDS: MICROSPORANGIATE STRUCTURES AND PHYLOGENETIC IMPLICATIONS[1]

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ABSTRACT

The microsporangiate structure of cycadeoid cones seems to have been composed of a fleshy portion, continuous and cup-shaped below and with separate distal members, each with a fleshy appendage at the distal region. This microsporangiate structure was probably derived from a phyletic fusion of separate sporophylls, the tips of which are still free, although compactly appressed to each other. Such an interpretation brings the cycadeoid cone closer to the williamsonian cone structure. Furthermore, certain cycadeoids seem to have had monosporangiate fruiting structures, including a cone described in this paper with only microsporangia, — another parallel with the williamsonias.

INTRODUCTION

EVEN though many strides have been made in attempting to interpret the cones of the genus *Cycadeoidea*, many gaps still remain, and at present only the general aspects are known. One thing that has become clear is that cones of *Cycadeoidea* were not elaborate, flower-like structures with a whorl of pinnately compound microsporophylls as postulated by Wieland (1906). In 1963 I suggested that, instead, there was a conical, ovulate receptacle surrounded by a massive, fleshy microsporangiate structure (DELEVORYAS, 1963). Cross sections of the microsporangiate structures seemed to indicate that the outer portion was a continuous zone of tissue, enclosing a system of rod-like structures on which were borne the synangia. While such an interpretation seemed to fit the sectional appearances of cones more closely than did Wieland's reconstruction, a number of difficulties remained. For example, the ontogeny of a cone such as the one I proposed would indeed be a puzzle. It is hard to imagine how such a dome-shaped structure could have developed as a closed structure containing within it the ovulate portion.

Another problem involves the relationship of a cone such as the one I showed in reconstruction with other cycadeoidalean (bennettitalean) genera. While I am not compelled to demonstrate any relationship (or, for that matter, to expect any relationship to be there), one feels more comfortable about his reconstruction if there is some kind of similar form to which he may compare his. In that connection, Wieland's cone reconstruction seemed to tie in more neatly with the Bennettitales than does mine; Wieland's "microsporophylls" resembled quite closely certain of the microsporophylls of the genus *Williamsonia*. The microsporangiate *W. spectabilis*, for example, consists of a cup-shaped structure with free tips on which were borne pinnae bearing microsporangia.

The main reason for the difficulty in describing just what a cone of *Cycadeoidea* looked like is the preservation of the material. Many of the sections of cycadeoidean cones are extremely attractive, at times spectacular. When examined with higher magnification, however, the details become fuzzy and it is not always possible to tell as much about the structure as one would like. Faulty preservation was at least partly responsible for some of Wieland's interpretations. And, I must confess, inadequate preservation has prevented me from telling all of the details of cone structure and has actually led me to some errors.

DESCRIPTION AND DISCUSSION

New information obtained from another trunk in the Paleobotanical Collections in the Peabody Museum of Natural History at Yale University has made it possible to

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correct some of these errors and to further our knowledge of cone structure. This trunk (No. 559) is listed as *Cycadeoidea Jenneyana*[2] in the catalogue, originating from a locality "near [the] Black Hills, S [outh]. D [akota]." The trunk is not complete, and preservation is variable over different parts of it. One of the cones in this trunk fragment, selected for longitudinal sections, is unique in representing, so far as we know, the only example of a microsporangiate cone with no evidence of an ovulate receptacle. Even though this cone is "atypical" in that respect, the microsporangiate portion has what may be considered "normal" structure. Because the preservation of this cone is quite dark in places it is possible to see certain structures clearly. As demonstrated earlier, the microsporangium bearing region is quite fleshy. Also evident, however, is the separation of this microsporangiate mass into a number of segments. The section in Pl. 1, Fig. 3 is a longitudinal one made to one side of the median plane. Much of the dome-shaped sterile tissue capping the microsporangium bearing region is preserved, and the divisions of the microsporangiate structure are quite evident there. Even though there is separation of the microsporangiate zone into what appear to be sporophylls, however, these sporophylls are extremely tightly appressed to each other. Also evident in slides of trunk No. 559 is an abundance of ramental hairs on the outer surface of the fleshy terminal extensions of the microsporophylls (Pl. 2, Fig. 8).

These fleshy members mounted on the sporophylls are what Wieland interpreted as paired abaxial "horns" on his compound frond-like pollen bearing structure. Wieland's conclusions were based largely on a cross section of the apical part of a cone figured by him in 1916 (Wieland, 1916, Pl. 57, Fig. 3). This section suggested that a number of V-shaped segments, representing paired horn-like appendages on the dorsal side of each sporophyll, extended beyond the fertile part of the sporophylls in the immature cone. A re-examination of this slide indicates that preservation of this part of the cone is distinctly inferior and that cellular details are completely obliterated. Furthermore, the V-shaped structures, as seen in cross section, are not regular and very likely represent mechanical or preservational breaks. It is quite clear from the new sections that there are not paired appendages at the tips of the microsporophylls, but single, fleshy units.

On the basis of sections made from trunk No. 722 described in an earlier paper (Delevoryas, 1963) it was concluded that the fleshy material at the top of the microsporangiate zone was a solid dome of tissue, and that there was no evidence of sporophylls in the cone. Critical re-examination of these sections, in light of what we know from the new sections with considerably more contrast, allows the possibility that the fleshy, sterile portion of the microsporangiate zone was composed of individual units, each mounted on a sporophyll. Separation into distinct wedge-shaped structures in cross section is difficult to demonstrate and almost impossible to photograph. The staining of tissue preserved in this region is extremely light, and preservation is not quite precise enough to show clear-cut divisions. Figure 2 (Pl. 1) is a photograph of part of that region and shows what might be interpreted as a division within the fleshy dome, obscure partly because of preservation and partly because the units were so tightly appressed. In fact, the sporophylls are pressed against each other so firmly that the composite aggregation of sporophylls resembles a fused mass. It might be argued that these cones are immature, and that at later stages of development separations between sporophylls were more distinct. This is a plausible suggestion, but I believe that separation between sporophylls was never considerable. Further evidence for such a statement will be presented below.

There is no doubt, however, that the microsporangiate zone was bounded externally by a continuous wall of fleshy tissue at lower levels. Many cross sections examined give no hint whatsoever of natural separations. Higher up, however, there seem to have been separations, but again obscured by the fact that these sporophylls were extremely tightly appressed. The level at which the sporophylls are free is about halfway between the base and tip of the cone.

2. Our knowledge of criteria by which to distinguish species of *Cycadeaidea* is still so unsatisfactory that in this paper there has been no attempt to determine the validity of this species name.

What, then, does the microsporangiate portion of a cycadeoid cone look like? A possible model might be a williamsonian cone such as that of *Williamsonia spectabilis*. The free portion of the cup-shaped microsporangiate structure might be imagined to have been bent inward, never having flared as did *Williamsonia*. Mounted on the top of each sporophyll was a fleshy projection, all of which formed a compact mass.

A number of problems remain concerning the precise details of the sporangium-bearing portion of the cone. Again, not enough well preserved cones are at hand, and only suggestions can be made. A cross section, relatively high in the fertile part of the cone, shows what are probably the free portions of the sporophylls (PL. 1, FIG. 4). From the peripheral sterile portion (main rachis) two sterile rod-like structures ("pinnae" of Weiland) project inward at the level represented by Fig. 4. Because these rods are not exactly at right angles to the outer portion of the sporophyll, not much of them can be seen in any one cross section. As Wieland recorded, on these rods of tissue are borne the microsynangia. Figure 5, (PL. 2) a radial section, shows some of these structures with sporangia suspended from the rods or "pinnae".

Tangential sections of the microsporophyll seem to suggest that there were two rows of these rods (PL. 2, FIG. 6) with sporangia suspended. Because these rod-like structures are inclined, a cross section of the cone may show two or three pairs of them at one level. Evidence seems to be that rods actually extended from the outer, peripheral part of the microsporophyll system to the inner, fleshy part immediately adjacent to the ovulate receptacle. Cross sections of the microsporangiate region, as in Pl. 2, Fig. 7, also suggest that the paired rods are connected from the outer part of the sporophyll to the inner face. In the figure the sections of paired rods are clearly visible. Cross sections such as this alone would not be enough to verify the suggestion of sporangium-bearing rods connected at both ends. When combined with longitudinal sections (note FIGS. 9, 10 in DELEVORYAS, 1963) they add more evidence for such an interpretation. Although this configuration is the one that seems the most appropriate on the basis of sections, attempting to determine how such a structure originated ontogenetically is quite difficult.

Earlier I gave evidence to suggest that the inner portion of the microsporangiate region was fused to the outer portion (i. e. the "tip" of Wieland's "sporophyll" was fused to the base of the rachis) (DELEVORYAS, 1963). This was not a feature universally present because some longitudinal sections showed these two parts quite separate. In view of the fact that so many longitudinal sections show these two parts free, and because only one slide showed otherwise, although apparently convincingly, there seems to be some doubt as to whether this fusion was real or simply only an illusion. Quite conceivably, the slide that showed this apparent fusion at the base was not an exact radial section in that region. And because the outer microsporangiate envelope is concave, an oblique section might possibly account for the configuration shown.

An interesting feature of the cones in trunk No. 559 is the massive size of the microsporangia. Some of the synangia attain a length of 5 mm. and a height (from proximal to distal end) of 2·5 mm. This differs considerably from sporangia in cones on trunk No. 722 which are quite small, seldom exceeding 2 mm. in length. Sporangia of the cones in trunk No. 214, illustrated by Wieland many times, are intermediate in size. The size of sporangia is not solely a function of age; it appears as if cones with small sporangia have many more of them than do the cones with massive sporangia. These differences in size and number of microsporangia may ultimately be an aid in taxonomic separation of cycadeoid species.

In summary, a cycadeoidalean cone, then, had (normally) an ovulate receptacle terminating a peduncle. Arising from the receptacle below the base of the ovulate portion was the microsporangiate structure. This structure was cup-shaped below, with no separation except at higher levels where fleshy, finger-like extensions projected from the margin of the cup. In other words, in ontogeny, the sporophylls began development as separate structures; at a later stage, an entire ring of tissue below developed zonally to raise the free tips. At the distal extremities of the sporophylls are fleshy, largely parenchymatous extensions, all of which in a cone are tightly appressed to give the appearance of a solid mass. Covering the surface is a dense mass of ramental scales. Rods of tissue arise from

either side of the flattened, or, in cross section, sometimes keeled sporophyll rachis and project downward and inward to the inner portion of the sporophyll. It appears as if most of the rods (or "pinnae") originate at levels above which the sporophylls are separate. There remains the problem of whether the inner portion of the sporophylls (that is, the portion adjacent to the ovulate receptacle) is continuous or discontinuous. It is impossible to answer that at present because it is possible to show a cross section in which these portions of the sporophyll are distinctly separate, and another where there is absolutely no indication of separateness (FIGS. 11 and 12 in DELEVORYAS, 1963).

Another problem that remains is the question of whether at maturity the cones opened into flower-like structures. If the parenchymatous dome-like structure were a solid mass as suggested by me in 1963, then it would be impossible for the sporophylls to separate and expand. Now that it seems more likely that the distal portions of the sporophylls were not attached to each other, it is logical to raise the question again of the mature situation in these cones. I still feel that it is improbable that the sporophylls expanded at later stages. For one reason, the trabeculate nature of the rod-like structures bearing the microsporangia would prevent such an opening. Attachment of these rods to both the outer and inner parts of the sporophyll would not allow expansion unless the attachment were somehow broken. There is other evidence that the cones did not open in another trunk in the Yale University collection. One of the cones (PL. 2, FIG. 9) sectioned longitudinally shows an ovulate receptacle with a mass of amorphous material above. That this material most likely represents the old microsporangiate region is suggested by the attachment of this material in a whorl to the peduncle just below the ovulate receptacle. There are occasional bits of old microsporangia visible as well. Furthermore, at the top of this entire mass are ramental scales attached to what was probably, the fleshy, sterile portion of the old microsporangiate region. This could represent an old cone, after the pollen had been shed (conceivably on the ovules of the same cone) with the pollen bearing organ in an advanced stage of distintegration. Other cones on the same stem are obviously further advanced ontogenetically and lack any remains of pollen-bearing structures. These are most likely cones that have lost the microsporangiate portions after pollination. If the cone with the remains of the microsporangiate region had "opened" at maturity, the old microsporangiate zone would not have been found in the condition in which it is preserved. Furthermore, the fact remains that there has still not been found any cone that shows the "opened" condition; the reconstruction of such a flower-like cone was based not on any actually found that way, but only on what Wieland felt the mature condition must have been.

Evidence seems to be accumulating that certain cycadeoidean cones were monosporangiate, i.e. only microsporangia or megasporangia (in ovules) were borne on a given cone. Many stems have ovulate cones that lack any traces of microsporangia, Even very young cones on some stems, obviously immature, show no pollen bearing structures. Strictly ovulate cones are not uncommon among the Williamsoniaceae, and a monosporangiate condition should not be entirely unexpected among the cycadeoids. Furthermore, the example cited in this paper of a microsporangiate cone, albeit only one, may be further evidence that monosporangy may be more common among the cycadeoids than previously envisioned.

More answers concerning the true nature of cycadeoid cones will be forthcoming when a few exceptionally preserved cones are located. It must be realized that our knowledge of the microsporangiate portion of the cone is really based on only a very few cones. Many seed bearing cones have been sectioned (although, even with these, certain details of seed structure are still vague), but there has not been even one cone with microsporangia preserved in what might be considered a completely satisfactory state.

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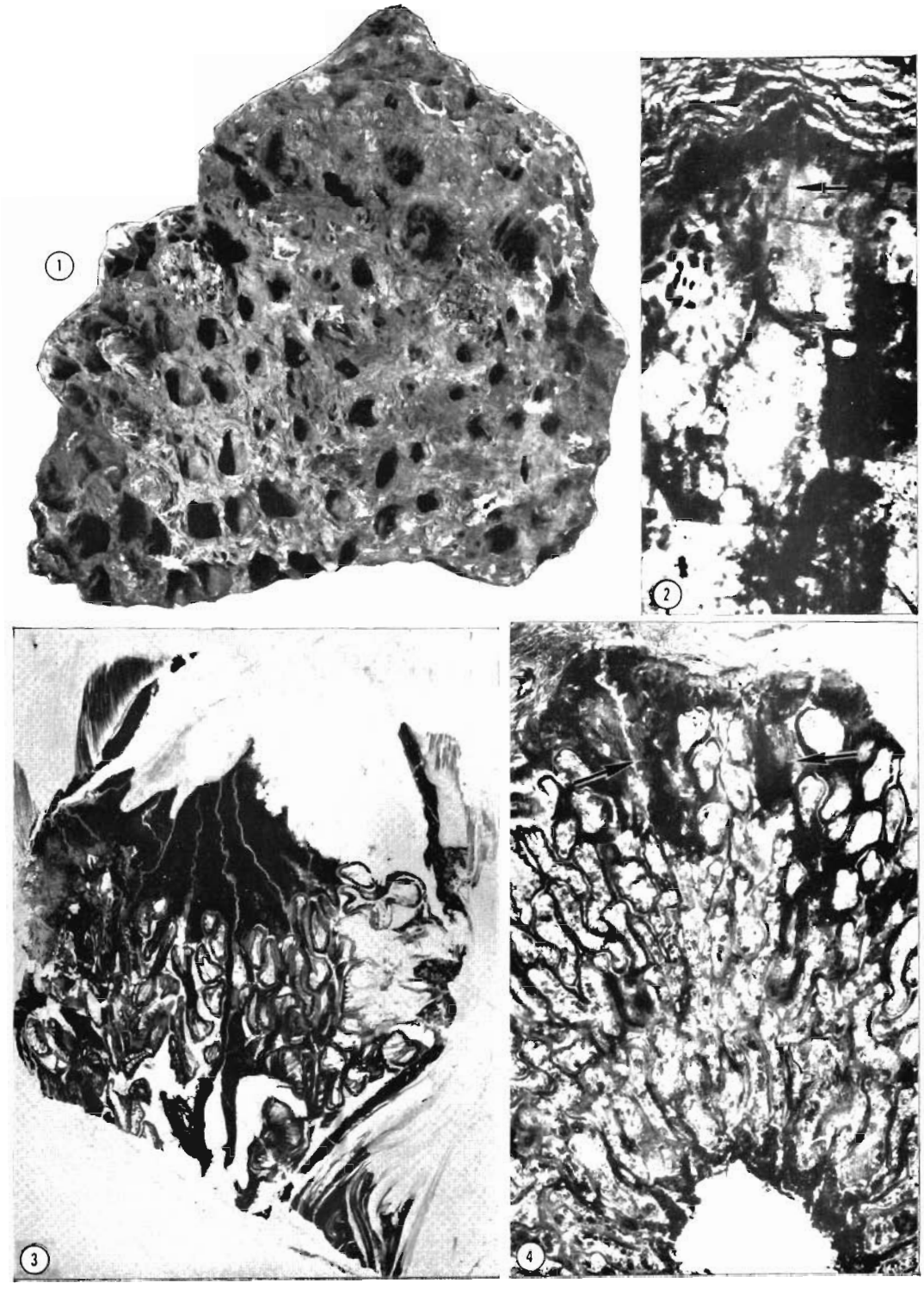
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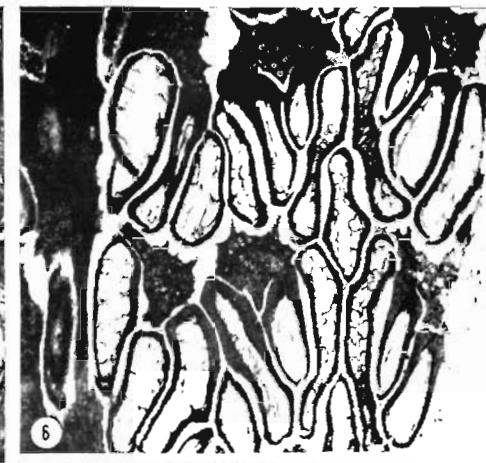
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EXPLANATION OF PLATES

PLATE 1

1. Trunk No. 559 in the Paleobotanical Collections, Peabody Museum of Natural History, Yale University. × 0·25.

2. Cross section of a portion of the sterile terminal part of a cone. Arrow indicates what may be a separation between two sporophylls. × 18·5. Slide NS 84.

3. Longitudinal section of a cone in trunk No. 559 not quite at the median plane. Separation of sporophylls is quite evident in the region of the distal fleshy members. × 2·4. Slide NS 89.

4. Transverse section of a cone in trunk No. 722 with two rod-like structures attached to the outer part of the sporophyll (arrows). × 8·4. Slide NS80.

PLATE 2

5. Radial section of a portion of a microsporophyll with sporangia borne on rods of tissue. × 7·6. Slide NS 97.

6. Tangential section through part of the microsporangiate zone. Sporangium bearing rods are sectioned transversely and show the suspended sporangia. × 8. Slide 302.

7. Transverse section of the microsporangiate region of a cone of *C. dacotensis*. Arrows at the top and bottom of illustration indicate the radial extent of a sporophyll. Pairs of rods on which are borne the sporangia are evident in the region between the arrows. × 6·4. (Unnumbered slide in the Wieland Collection).

8. Longitudinal section through the fleshy, sterile, terminal part of a microsporophyll with abundant ramental scales. × 5·2. Slide NS 96.

9. Longitudinal section of a cone from an undescribed cycadeoid stem. Arrow indicates the ovulate receptacle. Surrounding and above it is the disintegrated microsporangiate region. × 1·3. Slide NS 99.