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A PROBABLE PTERIDOSPERM WITH EREMOPTERID FOLIAGE FROM THE ALLEGHENY GROUP OF NORTHERN PENNSYLVANIA

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ABSTRACT

Compressed fossilized foliage most comparable to that of *Eremopteris zamioides* (Bertrand) Kidston occurs in shale associated with coal in the Allegheny Group in northern Pennsylvania. In association with this foliage are abundant samaropsid seeds and small, apparently microsporangiate organs. Although close proximity of disconnected plant parts as fossils is not evidence in itself that these plant parts were originally connected, it is tempting to believe that these leaves, seeds, and microsporangia were parts of the same species. Furthermore, there have been a number of previous reports associating samaropsid seeds with *Eremopteris*. Additional frondlike structures with the same basic construction as the vegetative eremopterid leaves have been found; these offer information concerning the possible mode of attachment of the fertile organs.

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Introduction

In his efforts to reconstruct plant life of the past, the paleobotanist is thwarted by the frequently fragmentary nature of plant remains in the rocks. It becomes essential to piece together these fragments into the proper whole by whatever valid means are available. Simple association of fragmentary plant parts in the fossil record cannot be used as definite proof that these parts were constituents of the same living plant. Obviously, the only conclusive proof involves organic connection or the demonstration that some peculiar or unique structural feature, such as that of the epidermis, is found in all the scattered parts. However, when associations occur with sufficient frequency, it is worth mentioning them and suggesting what the whole plant might have looked like if the pieces belong together.

Seward (1917, p. 170) figured a specimen of *Eremopteris artemisaefolia* (Sternberg) Schimper in close association with which are compressions of seedlike bodies referred to as *Samaropsis acuta* Kidson. This association was consistent enough for Seward to feel that the seeds were part of the plant that is known from these *Eremopteris* leaves. The seeds were flattened and bilaterally symmetrical, with two small distal hornlike projections.

Later Corsin (1928) described leaves like those of *Eremopteris zamioides* (Bertrand) Kidston from the Upper Westphalian of northern France. Associated with these fronds were fructifications that he assumed were part of the same plant that bore the leaves. Seeds, much like those figured by Seward (1917), were frequent, as were structures thought to be microsporangiate organs. These presumed microsporangia have small, radiating appendages, and look like small flowers. Parts of the foliage were also reported to have attached to them small, ovulelike structures in two rows along each pinna. These presumed ovulate structures, however, are immature and do not resemble the dispersed seeds. Corsin placed the entire assemblage into a new genus *"Pteridozamites"*, which he considered to be a pteridospermous plant.

Specimens of Carboniferous plants from Durham, England, in the Paleobotanical Collections of the Peabody Museum of Natural History include some *Eremopteris artemisaefolia*. On the same slabs, in close association with the leaf pieces, are bilaterally flattened seeds like those of *Samaropsis acuta* figured by Seward.

Thus, although nothing conclusive can be stated about the relationships of these vegetative and fertile plant parts, one is easily led to believe that very likely they belonged together, and that at least some species of *Eremopteris* were pteridospermous.

Description of New Material

Recent collections of Pennyslvanian plant compressions from northern Pennsylvania have further emphasized the possible relationship of platyspermic seeds and *Eremopteris* foliage. The material was collected in a strip mine about 4 km (2.5 miles) northwest of English Center, Lycoming County, Pennsylvania. The coal is thought to belong to the Allegheny Group and appears to be one of the easternmost outliers of that group in Pennsylvania. Plant fossils occur in a finely bedded gray shale that splits apart easily into thin sheets. Plant material is delicately preserved, although no cuticle appears to be present. Specimens are best examined submerged in xylene; photographs of the material included in this paper were taken in that fashion.

Common fossils at this site include *Sphenopteris obtusiloba* Brongniart and *S. spiniformis* Kidston, *Neuropteris heterophylla* Brongniart, *Lepidodendron obovatum* Sternberg, *Lepidostrobus* sp., and scattered *Lepidocarpon* megasporophylls.

Leaves of *Eremopteris* that closely resemble *E. zamioides* are extremely abundant. We believe that most of the specimens collected are entire leaves. They generally measure 14-20 cm in length; at the base of the rachis there seems to be a sharp line of abscission. Frequently, large numbers of these leaves are found closely aggregated, and all are extremely similar in general size and shape (Fig. 1). An alternative explanation of the abruptly truncated leaflike structures would be to regard them as pinnae of a much larger frond, the parts of which abscissed. Because most of the leaves found are the same size, and because it is difficult to visualize a pinnately constructed frond with pinnae identical throughout, we are inclined to regard these structures as entire fronds.

Pinnae are alternate to subopposite; the base of the rachis is generally naked, and lowest pinnae are smaller than the largest ones, which occur about half the distance up the rachis (Fig. 2). Largest pinnae may reach 5 cm in length. Pinnules are narrow

FIG. 1. *Eremopteris zamioides.* Slab with numerous leaves preserved. Intervals on scale at lower left are millimeters. YPM Paleobot. 1105. (Numbers refer to specimen numbers in the Paleobotanical Collections, Peabody Museum of Natural History)

FIG. 2. *Eremopteris zamioides.* Nearly complete leaf. YPM Paleobot. 1106.

and incised; pinnae at the distal end of the frond may be entire or occasional ones may have some incising. Venation is the open dichotomous type characteristic of *Eremopteris,* with no apparent midvein in the pinnules (Fig. 3).

Seeds found in close proximity to the *Eremopteris* foliage are conspicuously flattened and bilateral, with two prominent distal spines (Figs. 4, 5). They are quite unlike *Samaropsis acuta* seeds and resemble somewhat the seeds called *Ptilocarpus bicornutus* by Lesquereux (1879, Pl. 85, fig. 51) and later (1880, p. 565) *Cardiocarpus bicornutus.* This seed material, described by Lesquereux as having coniferous affinities, originated in the shale above coal in Coshocton, Ohio. In many respects these seeds resemble the Lower Carboniferous genus *Lyrasperma* Long (1960) from Scotland.

Shape of the new seeds is highly variable, perhaps partly due to natural variation and partly to varying degrees of compression during fossilization. Furthermore, these different shapes may represent different ontogenetic stages. A central oval or elliptical portion, possibly representing the outline of the inner testa, is discernible on the compressed seeds. A flange, or wing, surrounds this central body, as in many species of *Samaropsis.* This wing, of course, could represent either a true flangelike extension of the integument, or it may simply be the flattened sarcotesta after compression. Proximally, the integument is extended into an acuminate process, the end of which represents the point of attachment. Length ranges from 10 to 15 mm, and width from 4 to 6 mm in the primary plane (not including the distance between the flaring distal projections). In many specimens a conspicuous line runs axially along each of the flat faces. These lines could represent vascular bundles, or they may reflect the fact that the integument may be composed of two symmetrical halves (as in *Lyrasperma*), with the lines on the flat faces representing sutures.

Generally the seeds are in the form of thin, carbonaceous films, but rarely a megaspore membrane is present. One such seed (Fig. 6) had split along the major plane of symmetry exposing the spore membrane.

Possible microsporangiate organs associated with the foliage and seeds are similar to those decribed by Corsin (1928) for his "*Pteridozamites*" material. They are always found detached, most

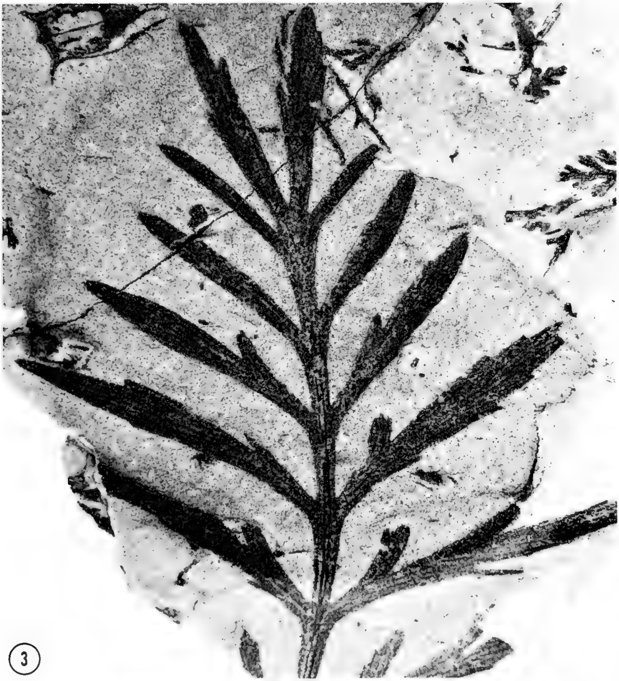

FIG. 3. *Eremopteris zamioides.* Terminal part of a leaf showing detail of venation. ×1.9. YPM Paleobot. 1107.

FIG. 4. Platyspermic seeds with distal hornlike projections and acuminate proximal region. ×1.3 YPM Paleobot. 1108.

FIG. 5. Platyspermic seeds in close association with a frond of *Eremopteris zamioides*. × 1.3. YPM Paleobot. 1109.

FIG. 6. Seed split along the primary plane to reveal the central megaspore membrane. × 11.5. YPM Paleobot. 1110.

likely after having shed pollen, scattered over the bedding plane surfaces, generally in clusters. In their mature state they look somewhat flowerlike or star-shaped, probably the result of a capsulate structure having split open at the time of pollination (Fig. 7). Maceration of these presumed fructifications, unfortunately, yielded no pollen grains.

If the associated plant parts described above are, indeed, detached organs of the same plant, we should suggest possible means of attachment, and what the entire plant might have looked like. Obviously, if the plant was actually a pteridosperm, by definition the reproductive structures must have been borne on leaves. There is nothing about the eremopterid foliage described thus far that indicates the possible mode of attachment. Very significant, however, are additional foliar structures, again in close association with the other parts, that are generally smaller than the typical vegetative leaves, but that have the same kind of construction, that is, a main rachis with pinnately borne laterals, oppositely or suboppositely arranged. On these laterals (pinnae) are short stubby projections that seem to be abruptly truncated as if representing structures from which some other bodies had fallen off (Figs. 8, 9). It is on just such structures that the seeds and pollen-bearing organs could have been borne. Furthermore, there appear to be at least two sizes of these presumed fertile leaves; the larger (up to 13 cm in length) could conceivably have represented the megasporophylls, while the smaller (generally about 5 cm long) could be microsporophylls. It might be argued that these presumed fertile leaves are actually immature vegetative fronds, and that subsequent development would have resulted in differentiation into the more typical eremopterid frond form. In the same beds, however, are specimens that are obviously immature fronds (Fig. 10), and in spite of their relatively young age they are conspicuously different from the probable fertile leaves and actually have much in common with the fully mature adult vegetative leaves.

Reconstruction

From these various parts, it is tempting to envisage a pteridospermous plant, perhaps not too tall, with eremopterid foliage borne on the stem. We conclude that these plants were deciduous, dropping the leaves in their entirety, although not necessarily at seasonal intervals. In most plants with fernlike leaves the fronds generally wither and shrivel before falling from the stem. These eremopterid leaves, on the other hand, appear to be little distorted, nicely flattened, with an abrupt truncation at the base of the rachis. Thus, the lower part of the plant would be naked, with functional foliage at higher levels. Elsewhere on the plant there may have been modified leaves, with the same structural plan as that in the vegetative leaves, but much reduced and bearing either microsporangia or seeds. A possible reconstruction of such a plant is presented in Figure 11. It must be emphasized, however, that this drawing represents only one of the several possible, logical combinations of the various structures.

Nomenclature

If, indeed, all of these parts are thought to belong to the same kind of plant, a single specific name should be used for the entire assemblage. Corsin considered his diverse plant fragments to represent portions of a single species to which he applied the name *"Pteridozamites" zamioides* P. Bertrand. However, for a number of reasons, this move cannot be accepted. First, there is no generic diagnosis in Corsin's paper for *P. zamioides,* hence the generic name is invalid. A second reason for rejecting the combination *P. zamioides* P. Bertrand is that Bertrand did not institute the name. Third, Corsin had no more evidence than we do that all of these parts are pieces of the same plant. As mentioned above, one is tempted to believe that because of their constant association all the separate parts logically belong to the same plant, but more concrete evidence must be at hand to prove the connection. If our new material consisted of remains only of the parts described in this paper, then it would be more certain that these parts are all from the same kind of plant. There is an abundance of other remains, however, including sphenopterid leaves, so there is also the possibility that the seeds and microsporangia were borne on leaves of that type. For that reason we have not formally assigned all of the parts to one name.

Discussion

Since we are not willing to agree with Corsin's assigning the various isolated parts of his material to a single name on the

FIG. 7. Possible microsporangiate structures. $\times 3.3$. YPM Paleobot. 1111.

FIG. 8. Possible microsporophyll, natural size. YPM Paleobot. 1112.

FIG. 9. Possible megasporophyll, natural size. YPM Paleobot. 1113.

FIG. 10. *Eremopteris zamioides.* Two immature vegetative fronds. Natural size. YPM Paleobot. 1114.

FIG. 11. Suggested reconstruction of a pteridospermous plant with eremopterid leaves and fertile structures such as those described in this paper.

grounds that the parts were not actually attached, we must justify our presumption in presenting the reconstruction in this paper. Certainly we are agreed that association in itself must be approached with caution. On the other hand, this is not the first time that the conspicuous association of platyspermic seeds with eremopterid foliage was noted. Reports by previous authors, together with this one, add up to evidence that cannot be dismissed lightly.

There is considerable precedent for the attachment of seeds to fernlike foliage in the Paleozoic. White's (1904) *Wardia fertilis* is an example of flattened seeds attached to foliage similar to that of *Adiantides. Emplectopteris triangularis* (Halle, 1927) is another example of platyspermic seeds borne on fernlike foliage, although in that case, seeds were borne on laminar surfaces. There are numerous other instances of seeds borne on foliage, but in most of the other reports, the seeds were radially symmetrical.

If such a plant as that suggested in our reconstruction did exist, what are its affinities? Platyspermic seeds are generally thought to be conifer-related, but the structure of eremopterid foliage is certainly far from a coniferophytic leaf morphology. Actually, bilaterally symmetrical seeds are an early type, having been reported by Long (1960) in the lower Carboniferous of Scotland. The fragments of axes on which are borne the various seeds with which Long worked are typically leafless, making it tempting to suspect that in some seed plants, at least, the seeds evolved *before* the appearance of leaves. If such is the case, it would be impossible to categorize these Mississippian plants as coniferophytes or pteridosperms. Eggert and Delevoryas (1960) suggested that bilateral symmetry of seeds need not be a reflection of natural affinities. *Conostoma* Williamson, a pteridosperm genus based on seeds with generally radial symmetry includes one species — *C. platyspermum* (Graham, 1934) — that is bilaterally flattened. Thus, platyspermic samaropsid seeds need not be considered uniquely coniferophytic, and their probable presence on eremopterid leaves need not be considered anomalous.

As work progresses on late Paleozoic and early Mesozoic pteridosperms, one cannot help but be impressed with the tremendous diversity of leaf types, seed structure, pollen-bearing organs, and vegetative anatomy. It is becoming increasingly obvious that the class Pteridospermopsida (or other nomenclatural equivalent) may ultimately be separated into a number of independent groups. Much parallel evolution of seed plants must have occurred during the Paleozoic, resulting in a number of groups of plants with fernlike foliage on which were borne seeds and pollen-bearing structures. The old class "Gymnospermae" has been shown to be an artificial assemblage (Arnold, 1948) with naked seeds being the only important feature in common. Similarly, we feel that before long the pteridosperms as they are now known cannot be held together as a natural entity solely by the character of seeds borne on fernlike foliage.

Acknowledgments

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