CARPANNULARIA RE-EXAMINED

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ABSTRACT

Carpannularia americana Elias is a synonym of *Annularia mucronata* Schenk, not *A. stellata* (Schlotheim) Wood. The suggestion that reproductive structures are attached to one specimen cannot be sustained. There is only a case for intimate association.

INTRODUCTION

IN 1931 Elias published the results of his investigations of some specimens of *Annularia* (California Academy of Sciences no. 2654-2656; collected near Clinton, Missouri). His most startling conclusion was that one shoot bore seeds, and he proposed a new genus, *Carpannularia*. Since that time there has been no demonstration of a further seed-bearing specimen, although the existence of a heterosporous equisetalean genus where development of the female gametophyte takes place within the megasporangium has been demonstrated (BAXTER, 1963, 1964). Abbott (1958, p. 324) mentions a globular structure on a specimen of *Annularia stellata* from Kimberley, Ohio, but this is not described, illustrated or interpreted.

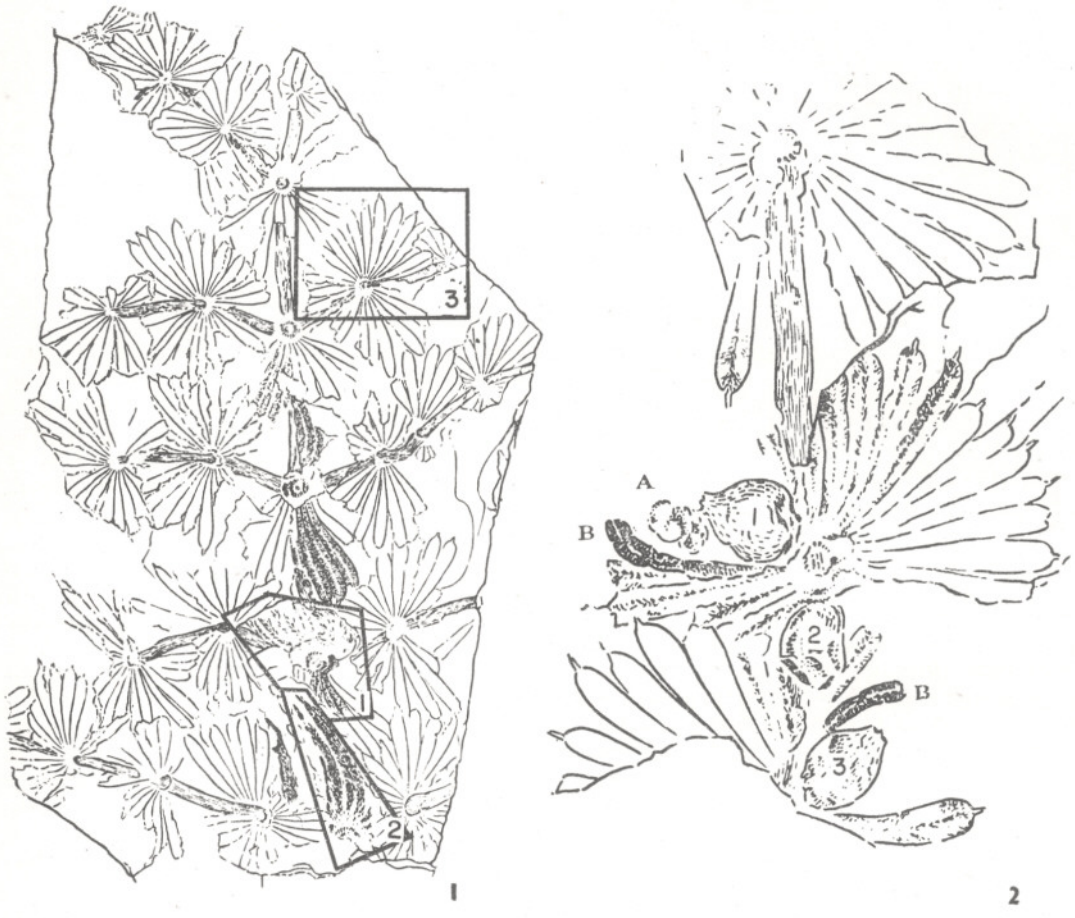
In dealing with Elias' contention, paleobotanical opinion has generally placated itself by drawing an analogy with the tubers produced on the subterranean stems of *Equisetum*, even though Elias' supposed seed-bearing shoot (ELIAS, 1934, PL. 15, FIG. 1; PL. 14, FIG. 3a) is perfectly acceptable as an aerial shoot and shows no obvious modification to a subterranean habit. Abbott (1958) apparently accepts this interpretation. Furthermore, she considers *Carpannularia americana* a synonym of *Annularia stellata* (Schlotheim) Wood. Abbott's interpretation is based upon Elias' paper and upon examination of one cotype specimen (no. 2654—this is cited as no. 87 by Abbott in the legend to her figure 87). Unfortunately, the specimen examined by Abbott is not the supposed seed-bearing specimen and it is the least informative of the three specimens.

The opinions presented here result from a careful examination of all three cotype specimens. These specimens were all examined and photographed while immersed in xylene or kerosene and illuminated strongly with oblique light. My main conclusions are: 1) that there is no evidence for the attachment of the supposed seeds to the shoot; 2) that the shoots are of a species of *Annularia* which has densely hairy spatulate leaves with mucronate apices, which I identify with *Annularia mucronata* Schenk rather than with *A. stellata*.

THE SEEDS

Although Elias (1934) did not always use the terms seed and fruit precisely, it is clear from the text that he considered that he was dealing with seeds. He described their rounded bases as provided with a short, broad extension by which they were connected to the node. When examined carefully under xylene no such basal extensions are visible. There is only a case for most intimate association, not for attachment.

Text-fig. 2 is a copy of one of Elias' extremely accurate and beautifully executed figures (PL. 15, FIG. 3a), into which I have inserted numbers for convenience of reference. Seed 1 (Pl. 1, Fig. 1) is most intimately associated with the shoot, but any suggestion of continuity is extremely ambiguous and I reject it. Examination of the base of this seed has been useful in demonstrating that there is a definite continuity of carbonaceous material between the base of the seed and the lamina labelled B in Text-Fig. 2, which was described by Elias as an abnormal leaf. This continuity does not establish connection of the seed to *Anularia* since B is not part of the leaf whorl and is definitely different in structure than the *Annularia* leaves. The *Annularia* leaves have a light brown delicate lamina with an opaque and more substantial vein. On the other hand, B is opaque and substantial across the entire lamina. Therefore my interpretation is that seed 1 has an



TEXT-FIG. 1. Modified version of Elias, 1931, pl. 13, figure 1a (California Academy of Sciences 2656). × 1. 2. Modified version of Elias, 1931, pl. 14, figure 3a (California Academy of Sciences 2655). × 2.

appendage of some substance and that no part of seed or appendage is attached to the *Annularia*.

Seed 2 dissolves in the nodal region into an amorphous patch of ochre. There are some flecks of carbonaceous material in the ochre but there is no way of telling whether they are from the seeds, the leaves, or the leaf sheath. As evidence for connection they are unconvincing.

Seed 3 is definitely unattached. There is a clear ragged line across its base. This seed is associated with a lamina (B in TEXT-FIG. 2) comparable to that which is attached to seed 1.

Although attachment of the seeds can be disputed, reinterpretation of them has been impossible. The relationship of a globular basal region and an attached laminate region is somewhat reminiscent of the structure seen in detached sporophylls of lycopods, but I must stress that I can make no precise comparison. I must emphasize that, although I follow Elias in referring to seeds, this is merely for convenience. No evidence has been produced demonstrating whether or not the structures are seeds and we know nothing of the contents of these organs. Elias suggested that an irregularly rounded brownish body (A of TEXT-FIG. 2) was the extruded interior of seed 1 and drew attention to other bodies of this kind scattered near the branch. These are iron stained irregularities in the rock and local centers of ironstone concretion. They are not fossils.

Elias enhanced comparison with branch tubers of *Equisetites burchardti* Dunker by describing the apices of the seeds as narrowed, somewhat like a bottleneck. This aspect was overemphasized. The apex of seed 3 is rounded in outline, while that of seed 1 is incomplete, although by projection it could be rounded (in addition, there may be some hairs in the apical region of seed 1, but this cannot be decided with certainty). The apex of seed 2 is missing.

THE FOLIAGE

Although Elias' accurate illustrations show leaves which are spatulate and mucronate, as in *Annularia mucronata* Schenk [the smaller-leaved *A. sphenophylloides* (Zenker) Gutbier can be excluded from consideration], Abbott identifies *Carpannularia americana* with *A. stellata*, a species with oblanceolate leaves. I believe she was influenced in this decision because the specimen she examined (no. 2654) is not the best for the determination of leaf shape, and because she was convinced that the specimen was glabrous. This hairlessness is an important consideration, because Abbott (1958) has been able to show that *A. mucronata* is hairy while *A. stellata* is glabrous. Elias (1931, p. 119) considered that the foliage of *Carpannularia americana* was covered with "truncate hairs, bristles or scales" (subsequently referred to by him as "hairs") appressed to the lamina and giving the leaf a feather-like appearance. He described these structures precisely and illustrated them clearly (*see* particularly ELIAS, 1931, PL. 15, FIG. 2). Abbott (1958) is entirely correct in reinterpreting these "hairs" as cellular arrangements of the adaxial epidermis. If only specimen no. 2654 were available (as it was to Abbott), then the argument for hairlessness in this species would be tenable. However, Elias also described some "brush-like appendages." These occur on a central branch of *Carpannularia* (*see* ELIAS, 1931, PL. 13, FIG. 1a, a modified version of which is reproduced as TEXT-FIG. 1). Elias believed they replaced leaves. He considered that each brush-like appendage consisted of delicate crowded hairs borne on an axis. Abbott (1958) simply ignores these appendages, making no attempt to interpret them. Critical examination of the specimen (PL. 1, FIGS. 4-7) shows that these appendages are foliage leaves which are densely hairy abaxially. The hairs are simple. They are borne at an angle of approximately 12 degrees to the midvein and measure approximately 800 × 30 μ. In life, such leaves were probably hispid below. This hairiness is continuous on the underside of the leaf sheath. Hairs are visible only where the overlying lamina and sheath are not preserved. Otherwise they are hidden.

While hairiness is at its densest on the leaf whorls of the central branch, it is also developed on the leaf whorls of the lateral branches. There, it is most easily seen where the hairs project beyond leaf apices (PL. 1, FIGS. 2, 3). These hairs are apparently longer than those on the lower parts of leaves of the central branch. Direct comparison of apical hairs cannot be made because no apices of leaves on the central branch are preserved. Although hairs can be seen lower on the leaves of the lateral branches, they are difficult to photograph. Without doubt they are less abundant than hairs on the leaves of the central branch.

On specimen no. 2655, a few hairs can be detected on some leaves of the specimen Elias illustrated on pl. 15, fig.3 a (TEXT-FIG. 2), but they are not very obvious and there is none on the leaf sheaths. This suggests that the specimen is one of the less hairy side branches. Other specimens of *Annularia* on the same piece of shale, somewhat larger than that illustrated by Elias, are markedly hairy, especially on the leaf sheaths. Protracted search of specimen no. 2654 has revealed only a few ambiguous marks which are possibly hairs. This does not prove that the specimen is hairless, since only the adaxial surface is visible.

DISCUSSION AND CONCLUSIONS

Carpannularia americana Elias is a name based upon sterile *Annularia* foliage lying in intimate association with some detached reproductive structures of unknown relationships. The sterile foliage may be identified with *Annularia mucronata* Schenk with which it agrees in size, leaf shape, and hairiness. The only other known hairy species of *Annularia* may be excluded from comparison. These are: (1) *A. fimbriata* Walton (1936), so far known only from the West-

phalian of Great Britain, which differs in its slightly smaller stature and in the possession of marginal rows of hairs instead of hairs covering the lower surfaces of the leaves; (2) *A. subradiata* Stockmans and Willière (*see* BOUREAU, 1964, pp. 183-184), from the Namurian of Belgium, which is a smaller and more delicate plant.

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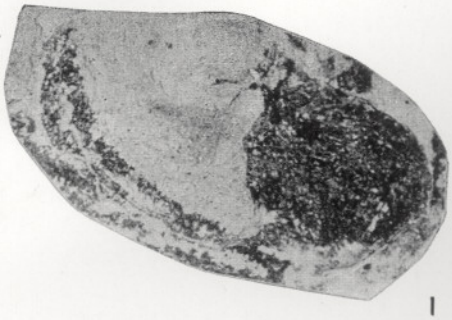
EXPLANATION OF PLATE 1

1. Seed 1 of Text-figure 2, × 10.
2. Leaf whorl included in area 3 of Text-figure 1, × 4.
3. Apex of leaf from whorl shown in figure 2 enlarged to show projecting hairs, × 10.
4. Enlargement of a portion of figure 5, × 10.
5. Leaf whorl included in area 2 of Text-figure 1, × 3·5.
6. Enlargement of a portion of figure 7, × 10.
7. Leaf whorl included in area 1 of Text-figure 1, × 3·5.



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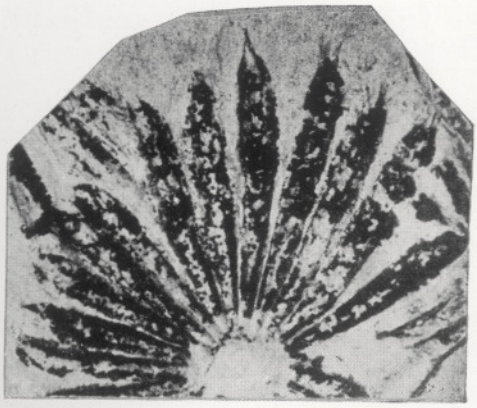

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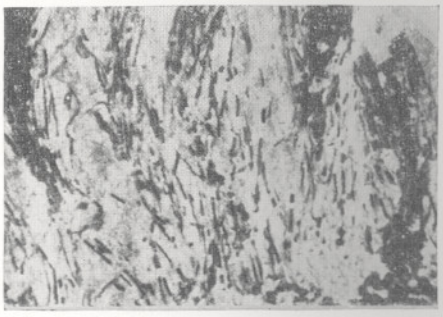

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