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CODONOTHECA AND CROSSOTHECA: POLLENIFEROUS STRUCTURES OF PTERIDOSPERMS

BY
WILLIAM C. DARRAH

THE PTERIDOSPERMS or seed-ferns are of especial evolutionary significance because in a number of structures they foreshadow the cycads and higher seed-plants. The main interest in the pteridosperms centers in their mode of fructification which is generally considered to be non-strobiloid, having true seeds and typical archi-gymnospermous pollen in sacs borne on pinnatifid branches of fern-like habit.

One of the important and meagerly known microsporangiate form-genera is *Codonotheca* which belongs to the medullosan seed-ferns.

Halle (7)¹ has published the only comprehensive survey of pteridosperm fructifications and has given direction to the interpretations concerning the polleniferous structures.

It was Sellards' (14) opinion that *Codonotheca* was the polleniferous structure of *Neuropteris decipiens* Lesqueux (11). I am inclined to this opinion because of the similarity of cuticular and stomatal structures of *Codonotheca* to those of *Neuropteris decipiens*. There is also some resemblance of its cuticle to that of *Neuropteris rariner-*

¹Italic numbers in parentheses refer to Bibliography.

EXPLANATION OF THE ILLUSTRATION

CODONOTHECA CADUCA *Sellards*

Upper figure: A cluster of synangia showing their paired arrangement. Carboniferous: Allegheny Formation. Mazon Creek, Illinois. Four fifths natural size. Harvard Botanical Museum (Paleobotany) No. 24991 (F.O. Thompson Collection).

Figure at lower left: Photograph of a nitrocellulose peel from one synangium. Note the orientation of the many small dark "granules." These granules are pollen-grains. Twice natural size. Mazon Creek, Illinois. Peeled from specimen No. 5033 Harvard Botanical Museum (Paleobotany) (Lesquereux Collection).

Figure at lower right: A single synangium natural size. Mazon Creek, Illinois. Harvard Botanical Museum (Paleobotany) No. 5026 (Lesquereux Collection).



vis Bunbury (3). It is well to note that Stockmans (15) identifies the Mazon Creek representatives of *Neuropteris rarinervis* with *Neuropteris attenuata* Lindley and Hutton. However, I am inclined to dismiss *Neuropteris attenuata* as of no more than varietal importance.

In the Lesquereux collection there are one hundred and thirty specimens of *Codonotheca caduca* which were identified as *Equisetites occidentalis* (11). Since there are certain calamarian leaves also included in the type series of Lesquereux, Sellards' name should stand and no attempt should be made to reinstate Lesquereux's specific name. There are sixty-two specimens of *Codonotheca caduca* in the F.O. Thompson collection.

Sellards had to deal with detached fructifications from which no evidence concerning arrangement could be obtained. I have illustrated in the first figure how the terminal sporangiate structures are borne pendulously on pinnatifid branches. There are four pairs of synangia arranged almost opposite. Several other smaller and more fragmentary branches are known, but these show the same opposite, pendulous and paired arrangement.

Each campanulate staminate structure has six long tubular sporangia filled with large pollen-grains imbedded in the tissue. In this respect, *Codonotheca* belongs to the same group as *Whittleseya*. Halle (7) interprets *Codonotheca* as follows: "Specimens of *Codonotheca caduca* of average size are stated to be 3-5 cm. long and 1½ cm. wide at the top. The segments are free for about half of the length of the specimen, or somewhat less. The spores are described as forming long and narrow groups which extend from the tip to the base of each segment and lie in more or less well-marked depressions occupying one half or two thirds of the width of the segment. Sellards states that there is nothing to indicate the location of the sporangia, but he evidently thinks that each group of

EXPLANATION OF THE ILLUSTRATION

CROSSOTHECA SAGITTATA (Lesquereux) Sellards

A specimen of a pinna, showing the typical sagittate form of the "sporophyll." Carboniferous: Allegheny Formation. Mazon Creek, Illinois. Three fourths natural size. Harvard Botanical Museum (Paleobotany) No. 19703 (F.O. Thompson Collection).



spores represents several sporangia 'more or less completely immersed in the tissue'. He discusses, however, a second possibility, namely that the segments themselves are enormous sporangia united at the base. This interpretation he rejects because of the great size of the segments and especially because of the vascular strands which are stated to run through them. In the light of the information which has now been gained regarding the structure of *Whittleseya*, *Goldenbergia* and *Aulacotheca*, I believe that this alternative interpretation is more probably the right one. The unusual size and shape of the spores and their aggregation in very long and narrow groups which form a uniseriate whorl round a central cavity are features characteristic of the three genera named, and if the sporangia, as believed by Sellards, are really immersed in the tissue, this would be yet another point of agreement." *Whittleseya* is a misunderstood form despite the lucid description given by Halle (7).

Recently Wodehouse (17) has revived the obsolete and erroneous opinion that *Whittleseya* is a ginkgoalean. *Whittleseya elegans* Newberry is the staminate fructification of *Alethopteris grandifolia* Newberry, (12) which Arnold has shown to bear *Trigonocarpus*-like seeds. *Whittleseya* is a pteridosperm of the order *Medullosae*.

The spores of *Codonothea* are very large, elongate-elliptical bodies 0.28–0.32 mm. long and 0.18–0.20 mm. wide. They retain a yellow resinous color sometimes obscured by reddish-brown stain. The spores usually contain two rather large dense structures which may represent nuclei. There are also present smaller irregular masses of a black substance which Sellards regards as the remnants of the original food supply. The pollen-grains of *Codonothea caduca* resemble those of *Dolerotheca fertilis* (7) in size, shape and ornamentation.

Sellards described (p. 89) the spores of *Codonothea*

as having a single longitudinal "slit". Misinterpretation of the material led him to this conclusion. It will be observed in the accompanying figures that *Codonotheca* spores have two furrows as have all other members of the *Whittleseyineae*. Halle remarks (p. 11) that these furrows "might be supposed to mark the junction between the part of the wall facing outwards in the tetrad and the two radial walls."

Codonotheca caduca Sellards seems to be restricted to the environs of Mazon Creek. It has been found at Mazon Creek, Braidwood, Wilmington and Morris. Somewhat similar, but not sufficiently preserved, specimens have been collected in the Upper Allegheny formation of Ohio and western Pennsylvania. Turner (16) has figured pollen grains found in the flame-etched surface of polished anthracite coal from the Ross coal of Nanticoke, Pennsylvania. The Ross coal is of Middle Allegheny age. It is impossible to identify this pollen specifically with that of *Codonotheca*, but there is no doubt that the pollen belongs to one of these medullosan fructifications.

Recently Chamberlain (4) has described *Neuropteris decipiens* as bearing *Trigonocarpus* seeds. He was led to this opinion by the celebrated reconstruction in the Field Museum of Natural History in Chicago. Professor Noe informs me that unfortunately the seeds have not been found in attachment. It is probably true that *Neuropteris decipiens* is a pteridosperm, that it bore polleniferous structures of the *Codonotheca* type and that it had seeds of a *Neuropterocarpus* or *Rhabdocarpus* shape and structure.

Crossotheca, unlike *Codonotheca*, is widely distributed and has figured prominently in phylogenetic speculations on the seed-forms. In addition, there are a number of points involved which stimulate reasonable doubt regarding the pteridospermous nature of at least a few species of *Crossotheca*.

Crossotheca is a spore-bearing form-genus defined by Zeiller in 1883, (18) and regarded by him to be filicinean. *Crossotheca* became known as the polleniferous member of the pteridosperms because a structure referable to *Crossotheca* was found in organic attachment with a frond type known to be seed-bearing. Within the past few years Crookall (5) has revived a long-standing controversy over this case, but before I discuss the issue it would be well to give a description of a typical species of *Crossotheca* for which the sterile form is also known.

Sellards (13) has described the attachment of *Crossotheca sagittata* (Lesquereux). The detached fructification had been named *Sorocladus sagittatus* by Lesquereux (11). For the sterile frond, Sellards cites the name *Pecopteris fontainei* Lesquereux MS., which was published without valid description by Lesley (10).

The small sagittate "sporophylls" bear 12 free, pendulous sporangia. These rather large sporangia have a length of 3–5 mm. and a width of 0.5–0.75 mm.

There are probably 128 spores to the sporangium (the lowest count in twenty-five well-preserved sporangia was 46, the largest 106). The spores are large, spherical bodies with a diameter ranging from 0.050–0.060 mm. All bear the typical tri-radiate scar, which in itself is not allowable as evidence in determining relationship. Sellards (13) states that the thick exospore is marked by minute warty thickenings. The spores in our preparations are almost smooth. Maceration methods used by Sellards may have slightly roughened (swelled) the exine, but this is not to be interpreted as a difference in opinion.

Crossotheca sagittata is borne on foliage of the *Pecopteris* type, long regarded to be true-fern. *Pecopteris fontainei*, the sterile form, belongs to the *miltoni-abbreviata* group, which finds a curious paradox in its known fructifications. The usual fertile form is *Asterotheca*, a typical

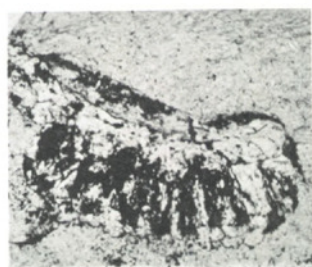
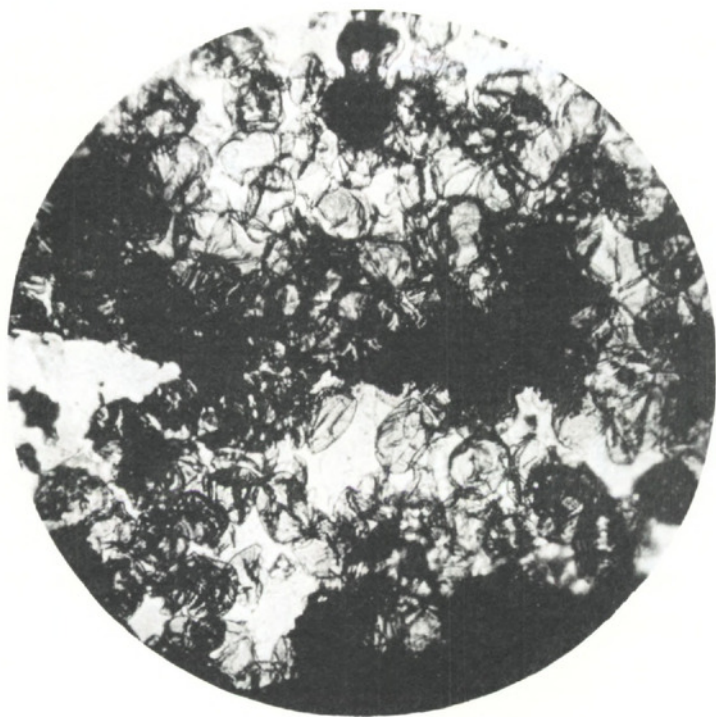
EXPLANATION OF THE ILLUSTRATION

CROSSOTHECA SAGITTATA (*Lesquereux*) *Sellards*

Upper figure: A small specimen from Mazon Creek, Illinois. Natural size. Harvard Botanical Museum (Paleobotany) No. 9748 (F.O.Thompson Collection).

Middle figure: "spores," somewhat collapsed, taken from the specimen shown in the upper figure. Photograph of a nitrocellulose peel. Magnified 75 times.

Lower figure: Photograph of a nitrocellulose peel showing a cluster of sporangia with the typical epaulette shape. Twice natural size. Mazon Creek, Illinois. Peeled from specimen No. 12192 Harvard Botanical Museum (Paleobotany). (Lesquereux Collection).



eusporangiate sorus with a prodigious production of very small ellipsoidal spores ($0.012\text{ mm.} \times 0.015\text{ mm.}$). Those species bearing *Crossotheca* fructifications have large spherical spores. Recently Halle (6) has found a species which he named *Pecopteris wongii* from the Permo-Carboniferous of Shansi Province of China. This species, clearly referable to the *miltoni-abbreviata* group, may prove to be seed-bearing. At least one specimen seems to have a single smooth rhabdocarp-like seed attached laterally. Halle is unwilling to accept this evidence without reservation.

The real reason why *Crossotheca* is held to be phylogenetically important is because it is believed to be the pollen-bearing structure of certain pteridosperms. To be specific, the microsporangiate fructification of the classic *Lyginopteris oldhamia* was believed by Kidston (9) to be a *Crossotheca*. Miss Benson (2) at once challenged this contention by showing how *Telangium* could as well be the microsporangiate structure of *Lyginopteris*.

Actually, Miss Benson has called attention to the weakest point in the argument, because the structure found by Kidston, though a true *Crossotheca*, does not belong to *Lyginopteris oldhamia*. The species has been renamed *Crossotheca kidstoni* by Crookall, (5) but it probably belongs to another lyginopterid.

It is interesting to note that *Telangium* shows a definite resemblance in structure to certain members of the *Whittleseyineae*. However, the evidence indicates that the synangium is bilaterally symmetrical.

Crookall (5) has shown that *Crossotheca* fructifications are borne on foliage of both the *Pecopteris* and *Sphenopteris* types, but he cites an opinion of Mr. Hemingway that in every case where proof of attachment can be obtained, this attachment has been pecopterid.

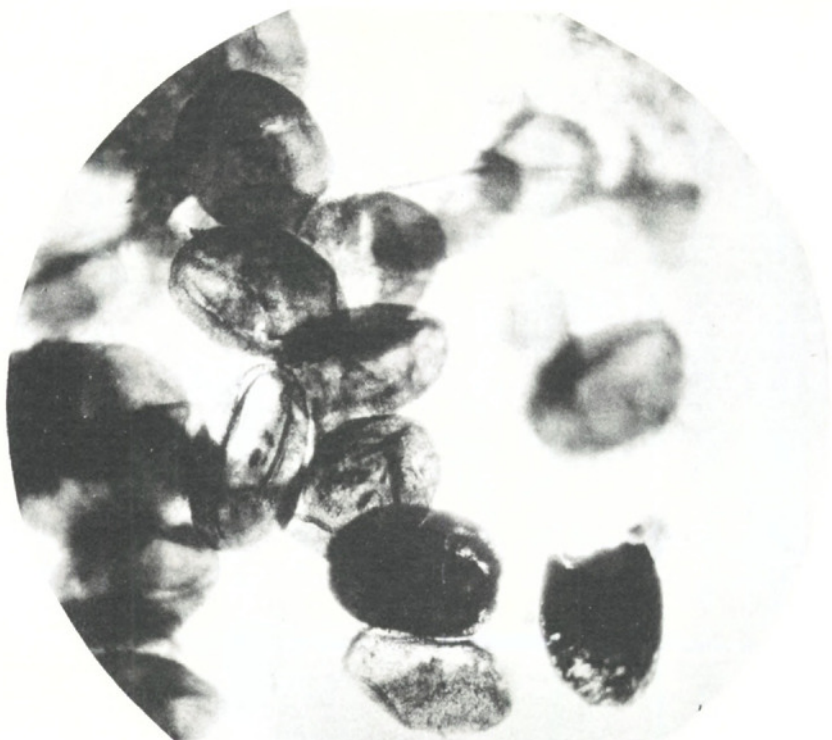
Hirmer (8) has arranged what he considers to be a

EXPLANATION OF THE ILLUSTRATION

CODONOTHECA CADUCA *Sellards*

Upper figure: Photograph of a nitrocellulose peel showing pollen-grains with the two furrows and the two dark bodies which bear some resemblance to nuclei. Peeled from specimen No. 5033. Photographed with a red filter.

Lower figure: Photograph of the same peel photographed without filters, showing apparently a single furrow.



phylogenetic series of micro-sporangiate structures beginning with the typical *Asterotheca*, then through *Asterotheca truncata* to *Crossotheca pinnatifida* to the typical *Crossotheca* to the *Whittleseyineae*.

It is not clear, however, whether this is only an implied transition from a typical fern synangium through pendulous encapsulated sporangia to the typical radial structure characteristic of the *Whittleseyineae*, or whether it is a genetically related series.

Thus we come to a brief consideration of the two genera under discussion: *Codonothea* and *Crossotheca*.

Codonothea is known to be a pteridosperm, its "pollen" (= microspores) are typically cycadean, and it belongs clearly to the *Whittleseyineae*.

Crossotheca is probably pteridospermous, but there remains the possibility that at least some of its species are filicinean. In *Crossotheca sagittata*, we may be dealing with a fern whose spores are typically pteropsid and are apparently unicellular.

The difference in spore structure may not be serious, for *Crossotheca* is attributed to the *Lyginopterideae*, the most primitive group of pteridosperms, while *Codonothea* belongs to the later-derived medullosans.

A careful investigation into the phylogeny and relationships of the seed-ferns reveals at once the scarcity of precise data. The order *Medullosae* is characterized by large ellipsoidal pollen borne in elongate, tubular sporangia, which may be fused into a seed-like synangium. On the other hand, from a survey of the available data and materials, it is not possible to circumscribe the limits of the *Lyginopterideae*, nor even to recognize with certainty the nature of their microsporangia. *Crossotheca*, although probably referable to the lyginopterids, may yet prove to be filicinean.

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