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OBSERVATIONS ON FOSSIL PLANTS FROM THE DEVONIAN OF EASTERN NORTH AMERICA

I. PLANT REMAINS FROM SCAUMENAC BAY, QUEBEC

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OBSERVATIONS ON FOSSIL PLANTS FROM THE DEVONIAN OF EASTERN NORTH AMERICA

I. PLANT REMAINS FROM SCAUMENAC BAY, QUEBEC

By CHESTER A. ARNOLD

ONE of the best-known Upper Devonian plant-bearing formations in North America is exposed in the cliff at Scaumenac Bay, between Miguasha Landing and Fleurant Point, along the southern shore of the Gaspé Peninsula in the Province of Quebec, Canada. This locality is most generally known for the abundance of fossil fish, and specimens from it can be found in museums the world over. The number of species of either plants or fish from this place is not large, but it is notable for the good state of preservation of the fish remains, the large number of specimens that may be secured, and the accessibility of the fossiliferous strata.

The cliff consists mostly of very fine grained sandstone and light greenish gray micaceous shales. Fossils occur at several levels, but plants are especially abundant in a sandstone layer two or three feet thick which outcrops almost one hundred feet above high tide and approximately midway between its eastern and western extremities (Pl. I, Figs. 1–2). In addition to plants this horizon contains remains of the crossopterygian fish, *Eusthenopteron foordi*. An incomplete specimen secured from it measured twenty inches in length.

These fossil-bearing cliffs, or the "Hugh Miller Cliffs," as they have been officially designated by the provincial government, are in a broad sense considered the equivalent of the Old Red Sand-

stone of the British Isles. The plant fossils indicate that the cliffs are more recent than the plant-bearing horizons of the Gaspé sandstones which are exposed at the eastern extremity of the peninsula, and are probably comparable in part to the Portage and Chemung formations in northern Pennsylvania and southern New York, where a similar flora also occurs. The stratigraphy and fauna at Scaumenac have been fully described by Clarke (1911) and by others, but, so far as the present author is aware, no figures or careful descriptions of the plants have been made since the original ones of Dawson. One of the objects of this account is to publish photographic reproductions of some of the plant types and thereby to facilitate comparison with similar material from other places.

No new species of fossil plants have been recognized at Scaumenac since Dawson announced their presence early in the last quarter of the previous century. He first identified a specimen of *Archaeopteris Jacksoni*, which was supposed at the time to have come from the Gaspé sandstone (1871). Later (1882) he described eight plant forms from Scaumenac which include, among others of doubtful affinity, *A. Jacksoni*, *A. gaspiensis*, *Cyclopteris Brownii*, and *C. obtusa*. *A. gaspiensis* was the only species from this locality to be described as new. Although frequent reference is made to these plants by subsequent writers, Dawson's original work still remains as the only contribution of importance, since no critical examination of the plants has been made within recent years. Arber (1912) and other paleobotanists have endeavored to compare European forms with the Scaumenac species on the basis of the brief and inadequate figures and descriptions, but with a degree of success which is only partial.

Other than the forms mentioned above and a few spore types the plant remains at Scaumenac consist mostly of indeterminable fragments of vegetation suggestive of drift material which had been subjected to prolonged destructive agencies. Apparently, the whole formation was deposited in open water which received the weathered products of some near-by igneous formation. Since the water was free from black mud or other repellent sediments, it was a favorable environment for large numbers of fish. The

fragmentary condition of the plants and the character of the matrix show that the plants had not grown *in situ*, but are probably the remains of débris which had floated seaward from the vegetation-mantled land not far away. The better-preserved specimens were probably carried directly to the place of deposition by the currents which bore the enclosing sand, whereas the more unrecognizable material had become stranded along the way for some time. Unfortunately, no petrifying minerals were present in the water, so that no appreciable amount of internal structure is preserved, although small bits of vascular tissue consisting of scalariform and pitted tracheids and other tissues may be observed in considerable quantity after disintegration of the rock by hydrofluoric acid. Remains of stems, some of which are as much as three inches in diameter and which show a large pith, testify to the occurrence of plants of considerable size on the adjacent land areas, but whether these indeterminable fragments have any connection with identifiable forms is unknown. The only determinable plant remains are detached leaves, leafy twigs, occasional branches bearing clusters of sporangia, and isolated spores.

The material constituting the basis of the present account consists of several specimens from Scaumenac in the Museum of Paleontology of the University of Michigan. A few of the specimens were secured by Dr. E. C. Case in 1915, and the remainder by Dr. B. M. Davis and the writer during the summer of 1934. It is advisable that more material from Scaumenac be studied before final conclusions pertaining to several things are expressed, but it is believed that the small collection at hand typifies the flora of that place and is comparable in many respects to that available to Dawson when the plants were first described.

1. *Archaeopteris obtusa* Lesq.

(Pl. II, Figs. 3–4.)

This species, which seems to be abundant at Scaumenac, was originally described as *Noeggerathia obtusa* by Lesquereux (1858), from Mauch Chunk, Pennsylvania. It was assigned to *Archaeopteris* by the same author in 1880 and to *Cyclopteris* by Dawson in 1882. Arber (1912) included it in the genus *Psygmophyllum*.

This latter assignment appears unjustified, and since the affinities seem to be with *Archaeopteris* it is proposed to retain the species within that genus.

Several of the specimens recently secured from Scaumenac agree well with a specimen from Pennsylvania figured by Lesquereux (1880, Pl. 49, Fig. 7) and with material from Scaumenac figured by Dawson (1882, Pl. 22). Dawson remarks on the resemblance between his material and that of Lesquereux. However, to judge from Lesquereux's figure, the Pennsylvania specimen more closely approximates the recently collected Scaumenac material than does the material Dawson figured, and the original figure of the species (Lesquereux, 1858, Pl. 1, Fig. 11) is quite like some of the smaller-leaved Scaumenac specimens (Pl. 2, Fig. 4). In some of his earlier works Dawson assigns to *A. obtusa* some material which apparently belongs to other species (1862, Fig. 33; 1871, Fig. 188).

The designation "*Psygmophyllum*" was applied to the species under consideration by Arber (1912) during an attempt to revise the genus. Not having seen material of *A. obtusa* and relying solely upon the figures of Dawson and Lesquereux as a basis, he proposed a specific diagnosis as follows: "Leaves of medium size, 3–5 cm. long and up to 4 cm. across, with long sheathing bases, spirally arranged on an axis, flabellate or obovate, (?) undivided, probably rounded at the apex. Nervation delicate, veins fairly close, with frequent dichotomies."

Arber is the first author to insist that the foliar organs of *Psygmophyllum* are spirally arranged with sheathing bases. Schmalhausen (1894) had previously interpreted *Archaeopteris Archetypus* from the Donetz basin in a similar way, but this was rather definitely disproved by Nathorst (1904), who showed that the pinnules of this species are arranged in the usual pinnate fashion. Whether or not this spiral arrangement exists in other forms referable to *Psygmophyllum* is not a matter of concern here, because the genus is not a natural one, but there is no evidence whatsoever that the pinnules of the Scaumenac species are spirally arranged or have sheathing bases. In several specimens the pinnate arrangement is quite evident (Pl. II, Figs. 3–4). Also, it

is apparent that the cuneiform bases of the pinnules converge to about the size of the axis and are laterally attached. The figures by Dawson and Lesquereux may not be decisive as regards this feature, but whenever the actual attachment can be seen in a specimen it is of the true pinnate type. The pinnules depart from the axis at a very acute angle and often lie appressed to it in such a manner that it is difficult to determine just where the point of junction is.

All the available Scaumenac material, consisting as it does of simple detached axes bearing obtusely cuneiform pinnules, gives no idea concerning the habit of the plant. A specimen figured by Prosser (1892, Pl. 2) from Phoenicia, Ulster County, New York, and assigned to *A. obtusa* by him has pinnules identical with those from Scaumenac, and also shows a portion of the branched frond. It has a central axis with portions of at least five pairs of lateral pinnae. The pinnae are probably opposite or subalternate, and interspersed between them are the rachial or interpinnate pinnules, as they are interchangeably called. This specimen shows the same mode of branching and represents every appearance of a typical *Archaeopteris;* hence the retention of that generic name for this species in preference to the indeterminate and nebulous designation "*Psygmophyllum.*" It is true that, until the fructifications of this plant are known, its affinities cannot be ultimately established, but *Psygmophyllum* is only an organ genus which exists solely for the reception of certain broad expanded leaves of unknown relationships, and to assign this species to it would be to disregard entirely the characters of *Archaeopteris* shown by the larger fronds. It certainly does no violence to our conception of *Archaeopteris* as a genus to retain *A. obtusa* within it. The fructifications, if known, might reveal relationships in other directions, in which case a new genus would have to be announced for its reception.

As is shown by the accompanying figures (Pl. II, Figs. 3–4), there are some noticeable differences in size of pinnules on separate pinnae. The specimen with the smaller pinnules (Fig. 4) seems to agree closely with the specimen figured by Lesquereux (1858, Pl. 1, Fig. 11) when he described the species. Prosser's figure of the

specimen from Ulster County, New York, seems also to resemble the smaller form. Whether more than one species is represented by the large and the small types cannot be stated at present, but it seems advisable to keep them together tentatively, at least. It appears quite reasonable to interpret the differences between them as environmental variations within a species or as differences of location on the plant.

It has been suggested that the pinnules of *A. obtusa* are deeply divided, but to judge from the material at hand, it appears that such division as is commonly observed is caused by a simple splitting of the large laminae during fossilization or by their having been lashed about by the wind during growth. Splitting usually occurs between the marginal crenulations and, in some instances (especially in Prosser's specimen), it appears that a certain amount of splitting might have occurred during growth as a result of lateral expansion of the pinnules.

Another feature common in this species is that the broad terminal portion of the pinnule is frequently wrinkled, with the wrinkles extending from the crenulate margin backward for nearly one half the length of the blade, where the surface gradually becomes smooth.

Nathorst (1904) remarks that the pinnules of *Archaeopteris Archetypus* from Ellesmere Land are symmetrical, like those of *A. hibernica* and *A. obtusa*, but he makes no reference to the rather marked similarity in size of the pinnules which one sees on comparing his figures with the last-named species. He does say that the pinnules of *A. gaspiensis*, of which he had material for comparison, are smaller.

2. *Platyphyllum Brownii* Dawson

Platyphyllum Brownii, a virtually unknown species, was described by Dawson (1862) from a fragment discovered at Perry, Maine. Among the material recently secured from Scaumenac there is but a single incomplete fragment that can be referred to it. These foliose structures have never been found attached to a stem, although Dawson (1882) interpreted certain structures from Scaumenac as showing evidence of attachment to a rhizome

or other prostrate structure. Arber (1912) considered this form close to *Psygmophyllum majus* from beds of probable Lower Carboniferous age in Newfoundland. It lacks sufficient diagnostic characters to warrant its inclusion in *Archaeopteris* as it is listed by Lesquereux in Volume III of the *Coal Flora* (p. 850).

3. *Archaeopteris Jacksoni* Dawson *and* *A. gaspiensis* Dawson

(Pl. II, Figs. 1–2; Pl. III, Fig. 3; Pl. IV, Figs. 1, 4)

Archaeopteris Jacksoni was originally described by Dawson from Perry, Maine, and was later recognized at Scaumenac (1872). Still later Dawson decided that most of the material which he had assigned to this species from Scaumenac was something else, so that a new species, *A. gaspiensis*, was named for its reception (1882). Dawson's account of these two species is confusing, but it appears that *A. gaspiensis* was supposed to have larger and less compactly placed pinnules than the other form. Among the Scaumenac specimens recently examined is a series of specimens, some of which seem to conform fairly well with the figures of *A. gaspiensis* (Pl. II, Fig. 2), but others show that specific distinctions are not definite, and it is impossible to assign some specimens to one rather than the other. The conclusion seems inevitable that the supposed differences cited by Dawson are merely variations within the species and of no diagnostic value. It should be stated, however, that Dawson seems to have realized this particular difficulty, since he states that separation of the two species is difficult in the absence of the spore-bearing parts.

Whether or not *A. Jacksoni* and *A. gaspiensis* are distinct species may depend ultimately upon whether their fructifications are different, as Dawson supposed them to be, which was his chief reason for separating them. He describes the spore cases of *A. gaspiensis* as being borne in pairs and sessile on the midrib, and those of *A. Jacksoni* as smaller and borne on forking veinlets. He does not state whether the fertile parts of either species were found attached to vegetative parts or whether they were merely in intimate association. This point will have to be settled before we are in a position to state clearly the relationship between the

two species, although White (1905), in discussing the matter, inclined to the opinion that, were the facts fully known, the species could no longer be considered separate. To judge from the material at hand, the present author is disposed to support this conclusion.

Among the material collected by Dr. Davis in 1934 is a fertile branch which seems to be of the same kind as those figured by Dawson from Scaumenac and by White from Maine, and referred to in each case as belonging to *A. Jacksoni*. The specimen consists of a rachis bearing portions of at least six pinnae made up of compactly placed fertile pinnules. These fertile pinnae are small, being scarcely more than 4 cm. long, although they are probably incomplete. They superficially resemble strobili with fairly rigid axes. The compact arrangement of the fertile elements and the attachment to a stout rachis is quite suggestive of *A. Jacksoni* (Pl. III, Fig. 4).

The sporangia from these fertile fronds vary in width from 0.23 to 0.43 mm., and in length from 1.5 to 1.9 mm. Their average dimensions are 0.3 × 1.7 mm. There are all gradations between these extremes of dimensions. Although Dawson does not give the size of the sporangia of *A. Jacksoni*, he does state that the larger sporangia of *A. gaspiensis* are about 3 mm. long. For this reason it is obvious that the sporangia whose dimensions are given here are consistently smaller than those assigned by Dawson to *A. gaspiensis*, and they are probably the same as those described by him for *A. Jacksoni*. Occasional smooth-walled spores, ranging from 73 to 93 micra in diameter, are to be found among the sporangia, but have not been observed inside.

The vegetative portions of *A. Jacksoni* are thoroughly described by White (1905), so that little need be said about them here. The rather small, closely set, overlapping, decurrent pinnules, which gradually curve outward from their points of attachment, seem to distinguish this species (with the possible exception of *A. gaspiensis*) from other American species. This dense arrangement of the foliage and the stout axes on which it is borne is suggestive of a slow-growing shrubby or bushy plant probably forming a thick mat of underbrush beneath larger shrubs and trees.

4. *Spores (Type G of Lang, 1925)*

(Pl. III, Figs. 1–2, 5; Pl. IV, Figs. 2–3)

When portions of the plant-bearing shales and sandstones are treated with hydrofluoric acid a considerable variety of fragmentary vegetable débris is secured. In addition to the smooth-walled spores mentioned in connection with the sporangia referable to *Archaeopteris Jacksoni* there are large-appendaged spores which appear identical in all respects with those found by Lang (1925) in the fishbeds of the Middle Old Red Sandstone at Cromarty, and also by Kräusel and Weyland (1929) in the Middle Devonian at Elberfeld, Germany. Lang was unable to associate these spores with any plant, but Kräusel and Weyland report them in association with *Aneurophyton germanicum*. The spores obtained from these three widely separated localities appear identical, especially as regards the peculiar grapnel-like bifurcations at the tips of the appendages (Pl. IV, Figs. 2–3) which Lang gives as the distinguishing structures of his Type G.

The Scaumenac spores vary in size from 120 to more than 200 micra in diameter, exclusive of the appendages, with a complete series of intermediate forms. On some of the largest spores the appendages may be simple, without the peculiar terminal bifurcations (Pl. IV, Fig. 5). These probably represent different forms. Although two or three spores are frequently seen adhering, no tetrad groups have been observed, as is reported for the spores from Cromarty. On the other hand, clusters containing large numbers (fifty or more) have been observed which suggest spore masses that have been released from sporangia with the spores still clinging together. The shape of these masses, however, is irregular, so that no idea can be obtained concerning the dimensions of the original containers. These masses are flattened by pressure, and the spores are held together by means of the interlocking appendages.

Certainly some significance may be attached to the occurrence at Scaumenac of the appendaged spores, although their affinities are not known. At Cromarty, where the type was first found, it occurs with Middle Devonian types such as *Hostimella* and

Palaeopitys. At Elberfeld the spores are associated with *Aneurophyton germanicum, Asteroxylon elberfeldense, Cladoxylon scoparium, Hyenia elegans, Calamophyton primaevum*, and other forms, indicating an overlapping of early and late Devonian floras. *Archaeopteris* does not occur at either of these localities, but the occurrence of this spore at Scaumenac suggests that there are some elements in common between the Middle Old Red and Elberfeld floras and the *Archaeopteris* flora of eastern Canada which are not yet fully known. Whether the Scaumenac beds are older than are commonly supposed or whether the Middle Devonian European types persisted during later times in the Western Hemisphere can be determined only after further investigations have been carried out.

Spores referable to Type G also occur with *Archaeopteris minor* at Pittston, Pennsylvania, in beds probably of Chemung age.

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PLATES I–IV

PLATE I

FIG. 1. Eastern end of Scaumenac Bay, looking northwest from Miguasha Landing. The plant- and fish-bearing rocks are exposed in the long, low cliff just above water level, in the central portion of the picture. The Bonaventure sandstone is shown high on the hillside in the middle and to the right.

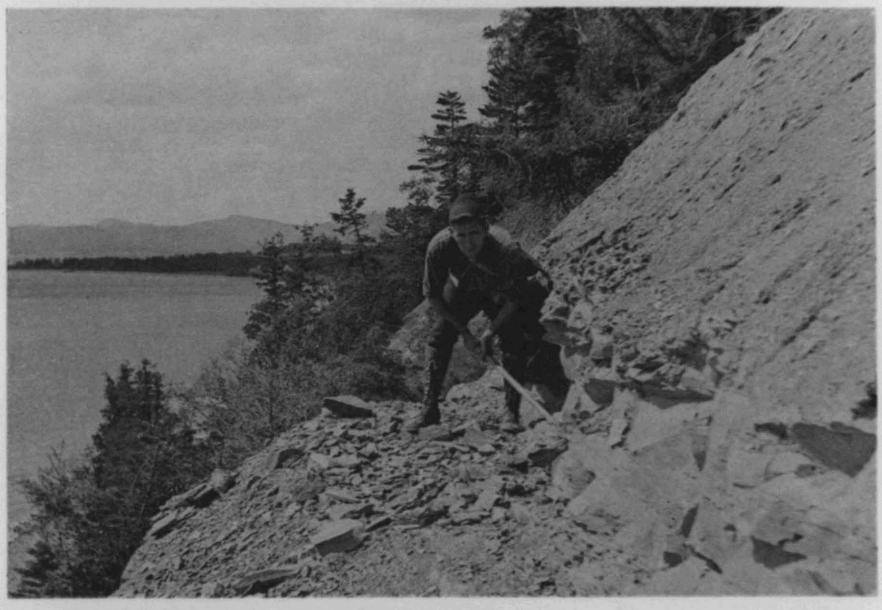


FIG. 2. Plant- and fish-bearing stratum near the middle of the cliff. About 100 feet above water level.

EXPLANATION OF PLATE II

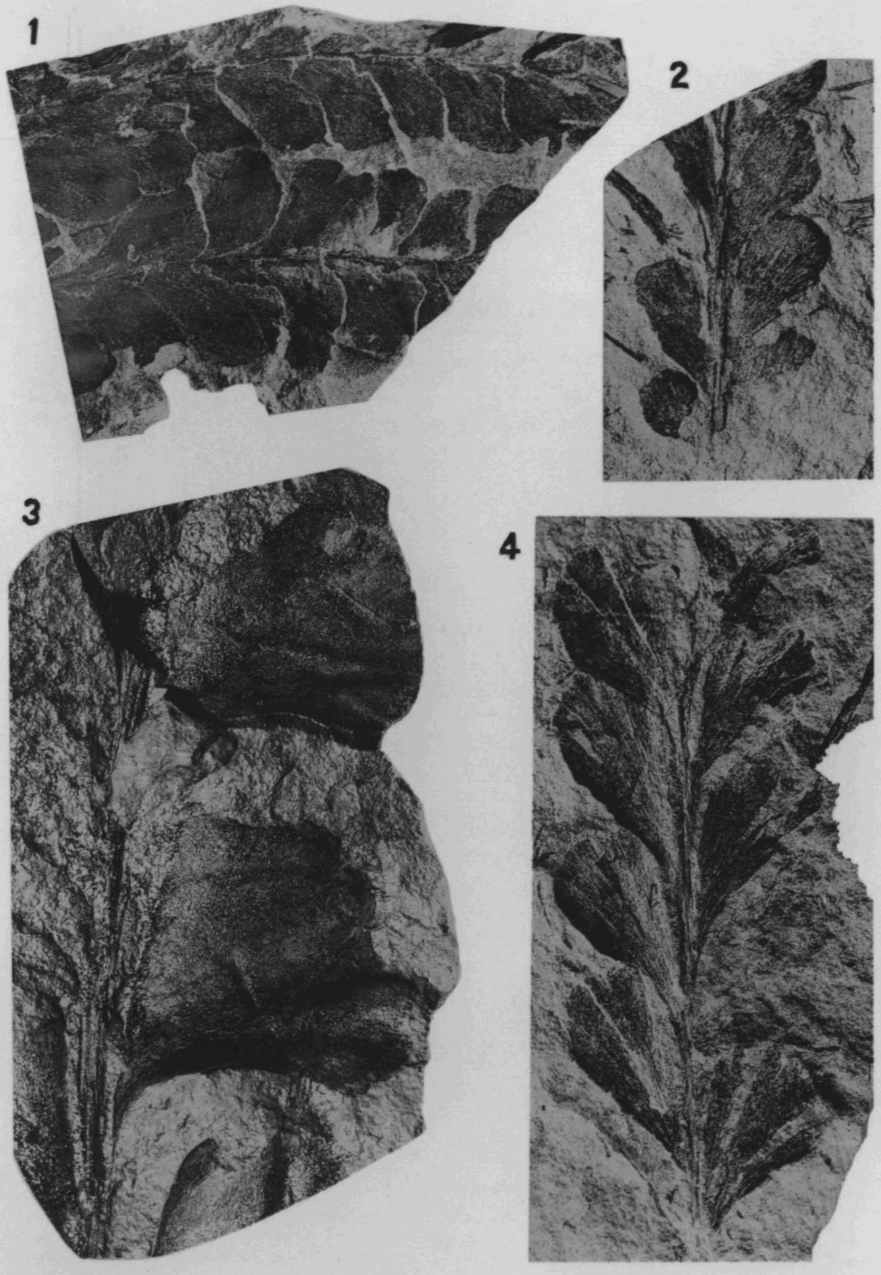
FIG. 1. *Archaeopteris Jacksoni* Dawson. Specimen showing characteristic overlapping pinnules

FIG. 2. *Archaeopteris* cf. *A. gaspiensis* Dawson. Specimen closely resembling Dawson's figure of type

FIG. 3. *Archaeopteris obtusa* Lesq. Portion of specimen bearing two large pinnules

FIG. 4. *Archaeopteris obtusa* Lesq. Specimen with smaller pinnules

PLATE II



EXPLANATION OF PLATE III

FIG. 1. Spore, Type G of Lang. × 120

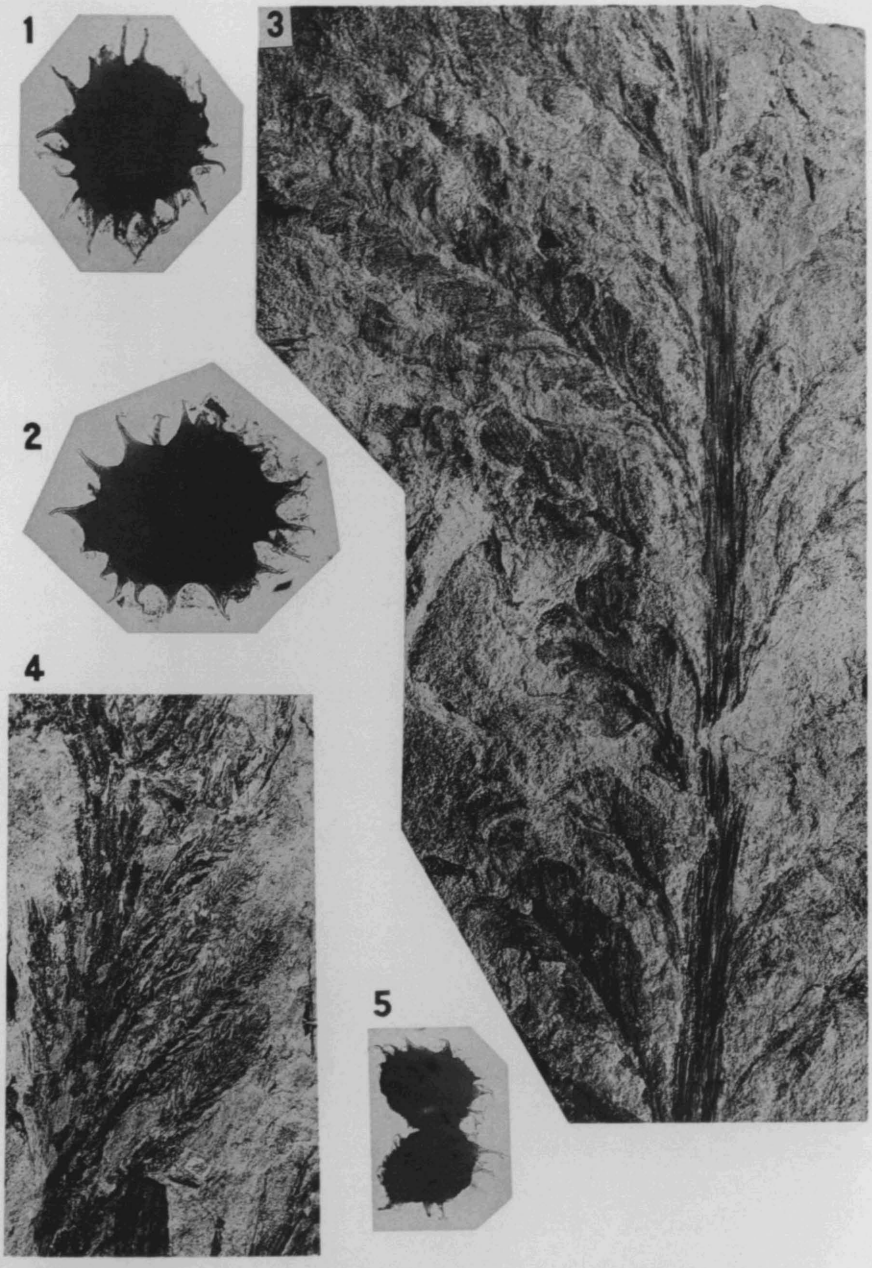
FIG. 2. Spore, Type G of Lang. × 120

FIG. 3. *Archaeopteris Jacksoni* Dawson

FIG. 4. Fertile branch, probably referable to *A. Jacksoni*

FIG. 5. Spores, Type G of Lang. × 120

PLATE III



EXPLANATION OF PLATE IV

FIG. 1. *Archaeopteris Jacksoni* Dawson

FIG. 2. Spore, Type G of Lang. × 120

FIG. 3. Spore, Type G of Lang. Tip of single appendage showing grapnel-shaped bifurcation. × 750

FIG. 4. *Archaeopteris Jacksoni* Dawson

FIG. 5. Undetermined spore. × 120

PLATE IV