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FOSSIL OPHIOGLOSSALES IN THE PALEOCENE OF WESTERN NORTH AMERICA[1]

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ABSTRACT

Vegetative and fertile frond segments of *Botrychium* have been recovered from Paleocene deposits of central Alberta, Canada. Specimens are preserved as coalified compressions that yield information about frond structure, sporangia, and spore ultrastructure. These fossils, described as *Botrychium wightonii* sp. nov., establish a megafossil record for the Ophioglossales, and demonstrate that modern-appearing species of the order were present in western North America by the earliest Tertiary. The largest vegetative fragments are up to 4.6 cm long and tripinnately compound, with opposite to subopposite branching. Ultimate segments are pinnatifid with dentate pinnules and open dichotomous venation. Fertile specimens are also tripinnately compound with a long rachis and subopposite to alternate pinnae. Sporangia are either submarginal and superficial, or marginal, and are all directed toward one surface of the pinnule. They are ovoid to subspheroidal and 0.8–2.0 mm in diameter. Some sporangia are apparently stalked, while others appear to be sessile. This variation results both from the ultimate frond segments being compressed in several different planes, and the fossils being exposed at different levels. Spores macerated from the sporangia are radial and trilete, and range 30–67 μm in diameter. Most are psilate, but some have a densely striate surface.

THE OPHIOGLOSSALES are a small order of homosporous, megaphyllous pteridophytes with three extant genera—*Ophioglossum, Botrychium,* and *Helminthostachys* (Tryon and Tryon, 1982). The order traditionally has been placed with the eusporangiate ferns, but the plants display an unusual combination of features, and their phylogenetic relationships remain obscure (Wagner, 1964). While some authors consider their relationship to ferns to be natural, others have suggested that they are descended from progymnosperms (Bower, 1926; Wagner, 1964; Bierhorst, 1971; Kato, 1988), and the vascular architecture in their frond has been compared to that of the conifer cone scale (Nishida and Higa, 1985). Among the most intriguing characters of the group are eustelic protoxylem architecture in *Ophioglossum,* a fertile spike (viz., sporophore) of equivocal homologies, putative secondary vascular tissue in *Botrychium,* and exceedingly large chromosome numbers in some species of *Ophioglossum* (Bower, 1926; Bierhorst, 1971; Tryon and Tryon, 1982).

Early workers interpreted several species from Carboniferous and more recent strata as representatives of the Ophioglossales (e.g., Seward, 1910; Scott, 1920), but all of these fossils subsequently have been reassigned to other groups (Taylor, 1981; Stewart, 1983). With the possible exception of dispersed spores of questionable affinities (Taylor, 1981), the Ophioglossales are generally considered to have no fossil record. Therefore, it is of significance that several vegetative and fertile frond segments (i.e., trophophores and sporophores, respectively) with the characteristic features of *Botrychium* occur in Paleocene deposits of central Alberta, Canada. These were figured and briefly described in a comprehensive treatment of the compression flora that occurs near Genesee, Alberta (Chandrasekharam, 1974). More recently, additional specimens have been discovered at the same locality, and spores have been extracted from the sporangia. These fossils provide a basis for documenting a sound megafossil record for the Ophioglossales in the earliest Tertiary of North America, and for demonstrating that essentially modern forms existed as early as the Paleocene. They also strengthen hypotheses of close similarities between the Tertiary floras of eastern Asia and western North America (Wolfe, 1981).

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MATERIAL AND METHODS—Specimens were collected from the Paleocene Genesee locality, located along the south bank of the North Saskatchewan River about 45 miles southwest of Edmonton in central Alberta, Canada (Chandrasekharam, 1974). The material was exposed by splitting loose blocks of shale that occur in the river bed. Spores were recovered from the coalified sporangial tissues by standard coal maceration techniques, demineralized in 48% hydrofluoric acid, rinsed in distilled water, and dehydrated into 95% EtOH. For scanning electron microscopy, drops of EtOH containing the spores were allowed to air dry onto specimen stubs, coated with 150 Å Au with a Nanotek sputter coater and photographed with a Cambridge S250 at 20 kV. All specimens are deposited in the Paleobotanical Herbarium, Department of Botany, University of Alberta (UAPC-ALTA).

SYSTEMATIC DESCRIPTION

Order: Ophioglossales
  Family: Ophioglossaceae
    Genus: *Botrychium*
      Species: *Botrychium wightonii* Rothwell et Stockey sp. nov.

Diagnosis—Pinnately dissected trophophore fragments and sporophores preserved by coalified compression; trophophore segments up to 4.6 cm long, tripinnately compound with subopposite to opposite pinnatifid, dentate pinnules. Pinnules with flexuous midvein and lateral veins that terminate near margin within obtuse to acutely pointed teeth. Sporophores up to 12.5 cm long with elongate rachis; tripinnately dissected distally with subopposite to alternate divisions and sporangia borne submarginally to marginally on narrowly laminar ultimate segments. Sporangia globose, 0.8–2.0 mm in diameter, sessile to stalked, with dehiscence slit. Spores radial and trilete, 30–67 μm in diameter, psilate to densely striate.

Holotype—Largest fertile specimen on slabs #S1336 (part) and S1333 (counterpart), showing mode of dissection, attached sporangia and spores; Fig. 1.

Paratypes—Fertile and vegetative frond fragments on slabs #S1333-S1336, S10534-S10536; Fig. 2–11, 13–17.

Collecting locality—The Genesee locality, south bank of the North Saskatchewan River approximately 45 miles southwest of Edmonton (53°21′N, 114°24′W) in central Alberta, Canada.

Stratigraphy—Buff to gray shale above Ardley Coal, Paskapoo Formation.

Age—Paleocene (Tiffanian).

Etymology—The specific epithet *wightonii* is proposed in memory of the late Dennis Wighton, paleontologist, University of Alberta, whose extensive collecting has added significantly to the paleobotanical collections.

DESCRIPTION—Numerous sporophores and several fragments of trophophores form the basis for describing *Botrychium wightonii.* Some of the fertile and vegetative fragments are intermixed (Fig. 1), but most of the sporophores are oriented parallel to one another throughout a small number of blocks (Fig. 2, 3), as if they had been growing and deposited together. Coalified remains of plant tissue are preserved on most specimens. Fragments of sporangia yield abundant spores (Fig. 14–17), but no cuticular remains have been recovered.

The largest vegetative segments are tripinnately compound, oppositely to suboppositely branched (Fig. 4, 5), and up to 4.6 cm long and 3.6 cm wide. These are comparable to the entire laminar region of the trophophore in some living species, but none of the fossils show evidence of either an elongated petiolar region or of the attachment of a sporophore. The largest fossils are also comparable in size and complexity to the primary pinnae of living species with larger fronds (e.g., *B. virginianum*), and we suspect the latter may be the more accurate interpretation.

Apical pinnules are lanceolate to ovate, and are simple and dentate (Fig. 4–6). They are up to 1 cm long. At progressively more proximal levels the pinnules become lobed and pinnati-

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Fig. 1–6. *Botrychium wightonii* sp. nov. **1.** Sporophore (holotype) surrounded by fragments of vegetative fronds. UAPC-ALTA #S1336 ×0.75. **2.** Sporophores oriented in the same direction in the matrix. UAPC-ALTA #S10536A ×0.67. **3.** Sporophores showing pinnate dissection and alternate arrangement of sporangia. UAPC-ALTA #S10536B ×1.25. **4.** Coalified compression showing largest specimen of tripinnately compound trophophore. Note opposite arrangement of pinnae. UAPC-ALTA #S10534 ×2. **5.** Impression specimen of tripinnately compound trophophore segment. Note subopposite arrangement of pinnae. UAPC-ALTA #S10534 ×2. **6.** Coalified compression specimen showing shape, dentition, and venation of pinnules. Note angle of divergence and decurrent bases of pinnules. UAPC-ALTA #S1335 ×12.


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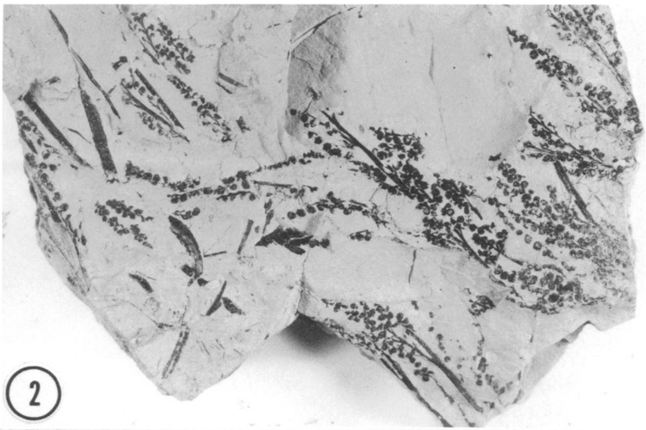
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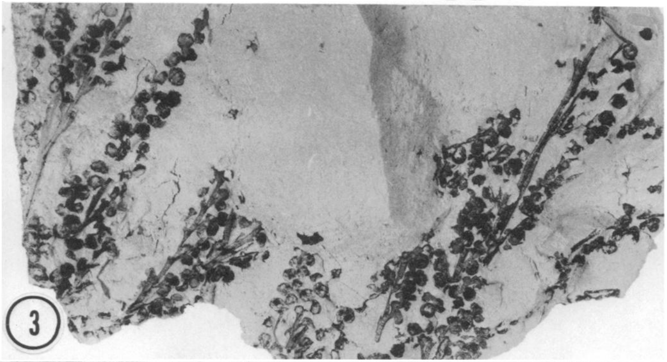
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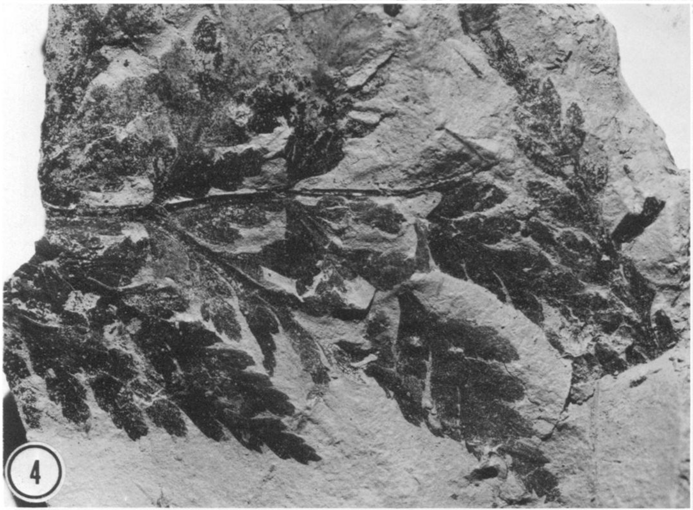
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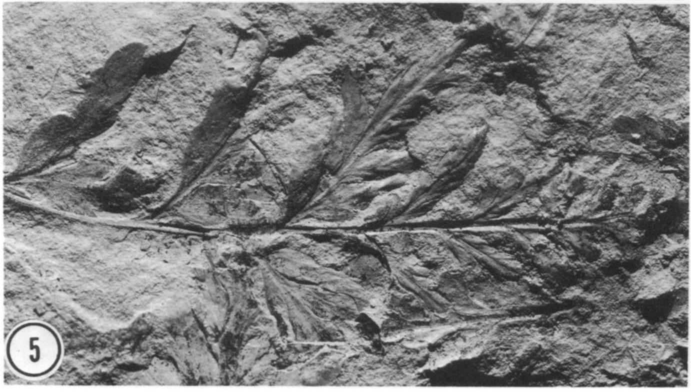
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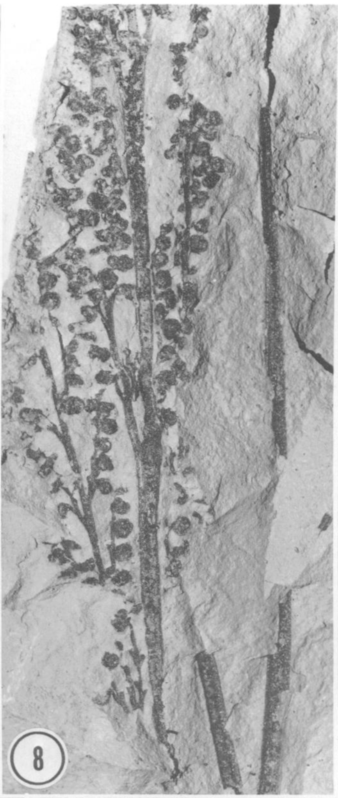
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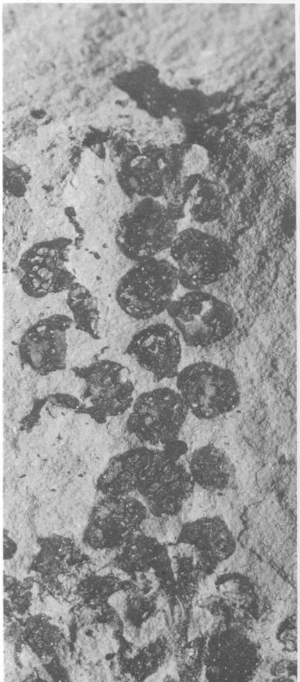
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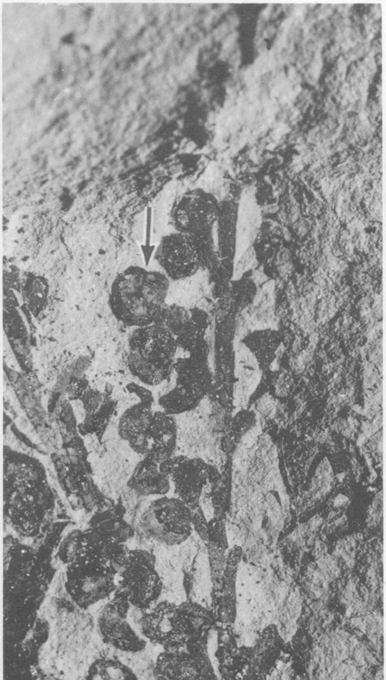
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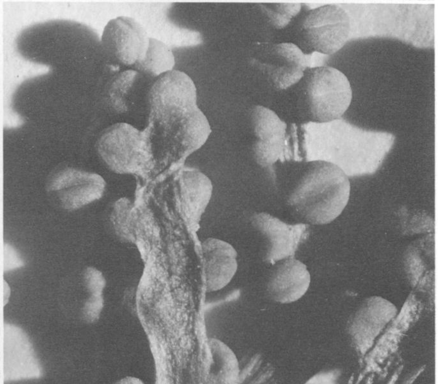
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fid, and then intergrade to a pinna rachis with lateral pinnules that are comparable to the apical pinnules (Fig. 4, 5). Individual pinnules diverge at 40–50° and are strongly decurrent (Fig. 6). A single vein enters the base of the pinnule and branches alternately to produce lateral veins that extend unbranched to a marginal tooth (Fig. 6). The midvein is straight near the base, distally becoming sinuous and flexing away from the points where laterals diverge (Fig. 6).

Sporophores are also tripinnately compound, but divisions are subopposite to alternate (Fig. 7–9, 11). The largest specimens are up to 12.5 cm long with an elongated, unbranched basal region 2.6 mm wide (Fig. 1, 7). The unbranched segment is comparable to the basal stalk on the sporophores of extant *Botrychium,* and indicates that the entire complexity of the sporophore is probably represented by the fossils. Lateral segments diverge at an acute angle (Fig. 8, 9, 11), and bear alternately arranged, globose sporangia (Fig. 10, 11).

The fossil specimens display a prominent range of variation in sporangial attachment. Some sporangia are broadly attached or sessile, while others appear to be stalked (Fig. 8, 9, 11). In some specimens the sporangia are attached to a pinnule segment in two rows (Fig. 11), while in others they appear to extend from only one side (Fig. 9). Still others show two rows of alternate sporangia, but the pinna to which they are attached is not in view (Fig. 10). This range of variation is difficult to explain if the sporangia of *Botrychium* are strictly lateral in attachment and oriented in the plane of frond dissection. However, an examination of several extant species reveals that they are not.

In extant species of *Botrychium* the sporangia are basically lateral, but they are not positioned in the plane in which the frond branches, and the distal rachial segments are not strictly terete. Rather, the rachial segments are narrowly laminar and the sporangia are all rotated toward one side. The lamina is more prominent in some species (e.g., *B. boreale,* Fig. 12) than in others (e.g., *B. virginianum*), but the sporangia of all extant species typically are curved or rotated toward one surface of the sporophore (Fig. 12). Some sporangia of the living species are broadly attached to the margin of the pinna, while others are submarginal (Fig. 12) and may be more narrowly attached. The sporangia typically display an apical dehiscence slit that is directed toward the side of the pinna to which the sporangia are rotated (Fig. 12). Dehiscence slits are obvious on dehisced sporangia, and may be prominent on mature sporangia (Fig. 12). On other relatively mature sporangia and immature sporangia the dehiscence slits are less distinct.

By comparing the fossils to this suite of features in the extant species, differences among the fossils can be interpreted to arise by the compression and exposure of a similar morphology in a variety of planes. As in the extant species, the sporangia of *B. wightonii* are all curved or rotated toward one surface of the sporophore. This is revealed by specimens that are compressed at right angles to the plane of rotation and exposed at the distal surface of the sporangia. In these, one sees two alternate rows of sporangia, but the pinna to which they are attached is not exposed (Fig. 10). Other specimens are compressed in the plane of rotation and exposed at the upper surface of the pinna. In these, one sees only one row of sporangia attached to one side of the pinna (Fig. 9). Still other specimens are compressed at right angles to the plane of rotation and exposed at the level of the pinna, so that the attachment of both rows of sporangia is revealed (Fig. 11).

Sporangia of *B. wightonii* are globose to subspherical, and range 0.8–2.0 mm in diameter. Some sporangia show a prominent dark line that represents the dehiscence slit (Fig. 11, arrow), but on many sporangia this feature is not

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Fig. 7–13. *Botrychium wightonii* sp. nov., Fig. 7–11 and 13, and *Botrychium boreale*, Fig. 12. **7.** Fertile specimen showing elongated, unbranched basal region and pinnate dissection. UAPC-ALTA #S10536A ×1.5. **8.** Apical region of tripinnately compound sporophore showing subopposite divergence of pinnae and alternate rows of sporangia. UAPC-ALTA #S10535 ×1.5. **9.** Sporophore with ultimate segments compressed from the side so as to reveal only one of the two rows of globose sporangia. Note stalked appearance of some sporangia. UAPC-ALTA #S10535 ×6. **10.** Fertile specimen with the ultimate segments compressed parallel to plane of division of the frond to reveal all of the sporangia oriented toward one surface. Pinna segment to which the sporangia are alternately attached is out of the plane at which the sediment split. UAPC-ALTA #S10536A ×5. **11.** Sporophore compressed parallel to plane of division of the frond and split at the level at which the sporangia are attached. Note globose sporangia with terminal dehiscence slit (arrow). UAPC-ALTA #S10536A ×5. **12.** Sporophore segment of *B. boreale* showing attachment and orientation of sporangia on ultimate segments, and shape of sporangia typical of extant species of *Botrychium.* Note dehiscence slits on distal surface of sporangia. ALTA #1 ×6. **13.** Fossil sporangium showing features of coalified surface (bottom and right), and attachment scar (arrow). UAPC-ALTA #S10536A ×28.

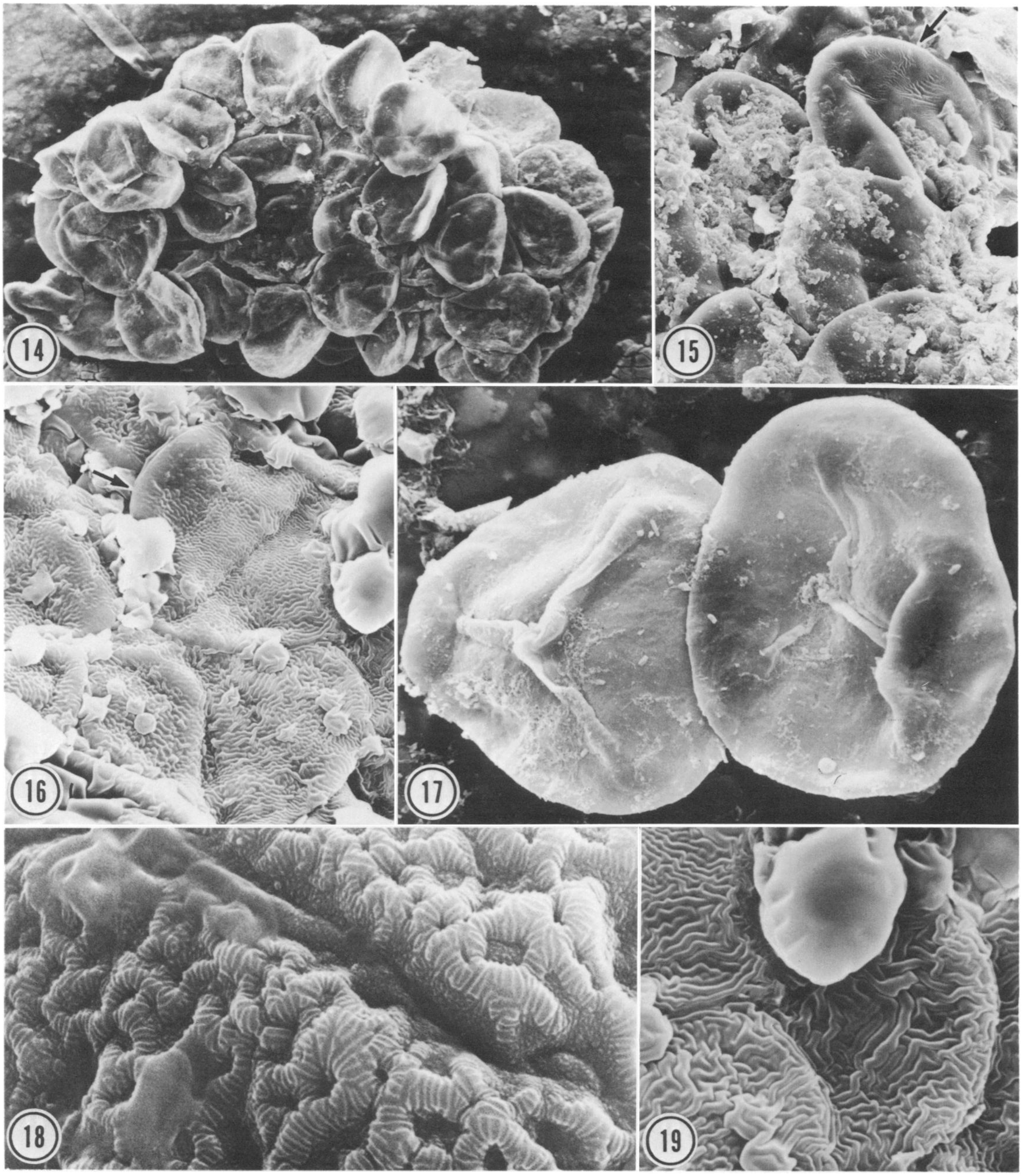

Fig. 14–19. Scanning electron micrographs of spores macerated from coalified sporangia of *Botrychium wightonii* sp. nov., Fig. 14–17 and 19, and spore of *B. lanuginosum*, Fig. 18. **14.** Mass of radial, trilete spores. ×290. **15.** Spores showing psilate surface in most areas, but weak striations are present in some areas (arrow). ×500. **16.** Spores showing striate surface. Note transition to psilate surface in some areas (arrow). ×775. **17.** Spores in proximal view showing trilete. ×1,000. **18.** Surface features of *B. lanuginosum*. ×5,200. **19.** Surface features of *B. wightonii*. ×1,500.

evident. The coalified surfaces of well-preserved sporangia display subtle striations (Fig. 13) that are comparable to the epidermal patterns in similar areas of living species. When the coal is removed from some sporangia, a circular scar that represents the point of attachment is exposed (Fig. 13, arrow).

Maceration of coalified sporangial material has yielded large masses of radial, trilete spores 30–67 μm in diameter (Fig. 14, 17). The number of spores per sporangim is difficult to determine because spores are not visible within the coalified sporangia until after maceration. However, there are as many as 80–100 in cleared sporangial fragments (e.g., Fig. 14) so several hundred spores must have been produced by each sporangium. Most spores are psilate, but those in a few preparations display dense striae (Fig. 16, 19). Most spores are largely psilate, but have some areas where striae are weakly developed (Fig. 15, arrow). Other spores with more highly developed surface features have small areas where the striae are only weakly developed or are absent (Fig. 16 at arrow). This continuous range of variation in surface features is consistent with developmental variations in spores of extant Ophioglossales (Lugardon, 1971), and we interpret all of the spores to be representatives of a single species.

It has been stressed that spore development in *Botrychium* is nearly synchronous (Wagner, personal communication), and this is consistent with our observations that variations in the spores occur primarily between fragments of sporangia rather than within a single fragment (cf. Fig. 14 and 16). According to this interpretation, the psilate spores (Fig. 14, 17) would be less mature than those with distinct surface features (Fig. 16, 19). If, however, the surface features of the spores represent perispore as they do in extant species of *Botrychium* (Lugardon, 1971), then their absence from many of the specimens may also have resulted from the harsh maceration treatments required to expose the fossil specimens.

In many of the preparations there are irregular globules among the spores and on the surface of spores (Fig. 16, 19). These give some psilate spores the superficial appearance of a rugose surface, but we interpret the globules to be tapetal residue of the type that is commonly found on the spores and pollen of both living and fossil plant material.

DISCUSSION—Based on the morphology of the trophophores and sporophores described above, these Paleocene fossils can be assigned to the genus *Botrychium* with a high level of confidence. Similarities in structure of the vegetative specimens and extant *Botrychium* fronds include pinnate dissection of planar frond segments, lanceolate to ovate pinnules with dentate margins and decurrent bases, pinnules with a single midvein, and with alternate, unbranched laterals. However, because even the largest trophophore segments of the fossils are isolated in the matrix, and show no evidence of either an elongated rachis or the attachment of the sporophore, it is not possible to determine with certainty if they represent the entire lamina of the trophophore or only a part of it. Therefore, the size of the frond, the overall shape of the trophophore, and the degree of trophophore dissection remain equivocal.

Sporophores of the fossil are even more diagnostic of *Botrychium* than is the vegetative material. The fertile specimens have an elongated unbranched rachis, pinnate dissection, alternately arranged sporangia, globose sporangia, and sporangia that dehisce by an apical slit. In addition, the sporangia are all oriented toward one surface of the planar sporophore, as is characteristic of *Botrychium.* Spores of the fossil are also radial and trilete like those of living *Botrychium* species.

The combination of characters discussed above is diagnostic of *Botrychium* and unlike all other eusporangiate ferns. It is also distinctly different from filicalean ferns, where the annulate sporangia are usually much smaller and have far fewer spores. There is a superficial similarity of the sporophores of *Botrychium* to the pinnate fertile spikes of some gymnogrammoid ferns, where the pinnules are enrolled to enclose one or more sporangia (e.g., *Anemia,* Bower, 1926). When the fertile pinnules of such ferns are compressed, they resemble a single sporangium of *B. wightonii* (Skog, 1982), but maceration exposes several leptosporangia. This is in contrast to *B. wightonii,* where the dehiscence slit (Fig. 11), attachment scar (Fig. 13), and some surface features of the sporangia are preserved on the surface of the compression fossils. Moreover, macerations of *B. wightonii* reveal large masses of spores from a single sporangium, rather than several sporangia.

The genus *Botrychium* is typically divided into four subgenera (Kato and Sahashi, 1977). As summarized by Tryon and Tryon (1982), the subgenera include *Sceptridium, Japonobotrychium, Botrychium,* and *Osmundopteris* that are distinguished by the structure of leaf buds, shape of the vegetative lamina, thickness of the pinnules, position of attachment of the sporophore, and surface features of the spores. Because most of these characters are not preserved in the fossils, assignment of our specimens to a subgenus is difficult.

In terms of the overall morphology of sporophores and trophophore fragments, pinnule shape, and pinnule venation, the fossils show a remarkable resemblence to the widely distributed *B. virginianum* (subgenus *Botrychium*). It also is interesting to note that *B. virginianum* grows in central Alberta today. On the other hand, the surface of the spores of *B. virginianum* is verrucate rather than striate as in the fossils.

The eastern Asian *Botrychium lanuginosum* (subgenus *Japanobotrychium*) is another extant species to which *B. wightonii* shows several similarities. In overall complexity (A. Tryon, personal communication) and in morphology of the trophophores and sporophores *B. virginianum* and *B. lanuginosum* are quite similar (Wagner, personal communication). However, the sporophore attaches much higher on the trophophore of *B. lanuginosum* than *B. virginianum.* This feature is unknown for *B. wightonii.* Like *B. wightonii,* the spores of *B. lanuginosum* are striate (Kato and Sahashi, 1977; Sahashi, 1980). However, the striae of *B. wightonii* form a regular pattern over the surface of the spore (Fig. 19), whereas those of *B. lanuginosum* are grouped into ridges that either form a reticulum (Fig. 18) or are more closely spaced (Sahashi, 1980).

The discovery of *Botrychium wightonii* in Paleocene sediments of Alberta provides the first unequivocal megafossil record for the Ophioglossales, and demonstrates that essentially modern species of the order were present in North America by the earliest Tertiary. Although the order is widely considered to be of great antiquity (e.g., Bierhorst, 1971), this is the first documentation that this supposition is essentially accurate. At the onset of this investigation, we hoped to find some primitive features of the fossils that would help clarify the phylogenetic relationships of the order. However, because the fossils are clearly so modern in appearance, systematic clues of this type have not been forthcoming. Nevertheless, the discovery that *Botrychium* was well differentiated by the beginning of the Tertiary does confirm the antiquity of the Ophioglossales, and allows us to focus future investigations of the evolution of the order in Mesozoic and Paleozoic deposits.

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